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Discordant Phylogeographic and Biogeographic Breaks in California Halibut

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Abstract.—The range of the California Halibut, *Paralichthys californicus*, spans three biogeographic provinces along the coastline of Alto (United States) and Baja (Mexico) California. To assess population genetic structure of the California Halibut, we analyzed mitochondrial cytochrome *b* sequences from 375 individuals across a large portion of its native range. Nucleotide diversity was consistently low among sampling sites ($\pi = 0.0026 \pm 0.0017$), while haplotype diversity was consistently high ($h = 0.77 \pm 0.024$). We found that California Halibut were genetically homogeneous across sampled sites with an overall $\Phi_{st} = 0.0030$ ($p = 0.22$). We saw no evidence of genetic discontinuities at two previously recognized marine phylogeographic breaks in the Los Angeles region or across the California Transition Zone at Point Conception. We conclude that California Halibut are genetically homogeneous and experience substantial gene flow, at least over evolutionary time scales.

INTRODUCTION

The nearshore marine environment of coastal California (USA) has long been a playground for biogeographers owing to its dynamic composition of marine organisms that has undergone dramatic shifts during the past five decades or so, particularly among marine fishes (Horn, *et al.*, 2006). While southern California's marine ichthyofauna was once thought to share many elements of the cool water "Oregonian" faunal assemblage, a persistent warming trend since the early 1980s precipitated a change in southern California's marine ichthyofauna to a more temperate, sub-tropical fauna with established communities whose biogeographic affinities lie with faunal assemblages further south along the Pacific Coast (reviewed in Lea and Rosenblatt, 2000).

While the biogeographic history of southern California is dynamic, one geographic feature has consistently stood out as a potential dividing point between two distinct faunal provinces at Point Conception, a prominent headland that marks the beginning of the "California Bight" and the California Transition Zone (CTZ; Figure 1 [Valentine, 1966]). However, as detailed distributional data on California's marine fishes emerged, this biogeographic "break" appeared to be "leaky", and is now regarded as more of a gradual transition zone (Horn, *et al.*, 2006).

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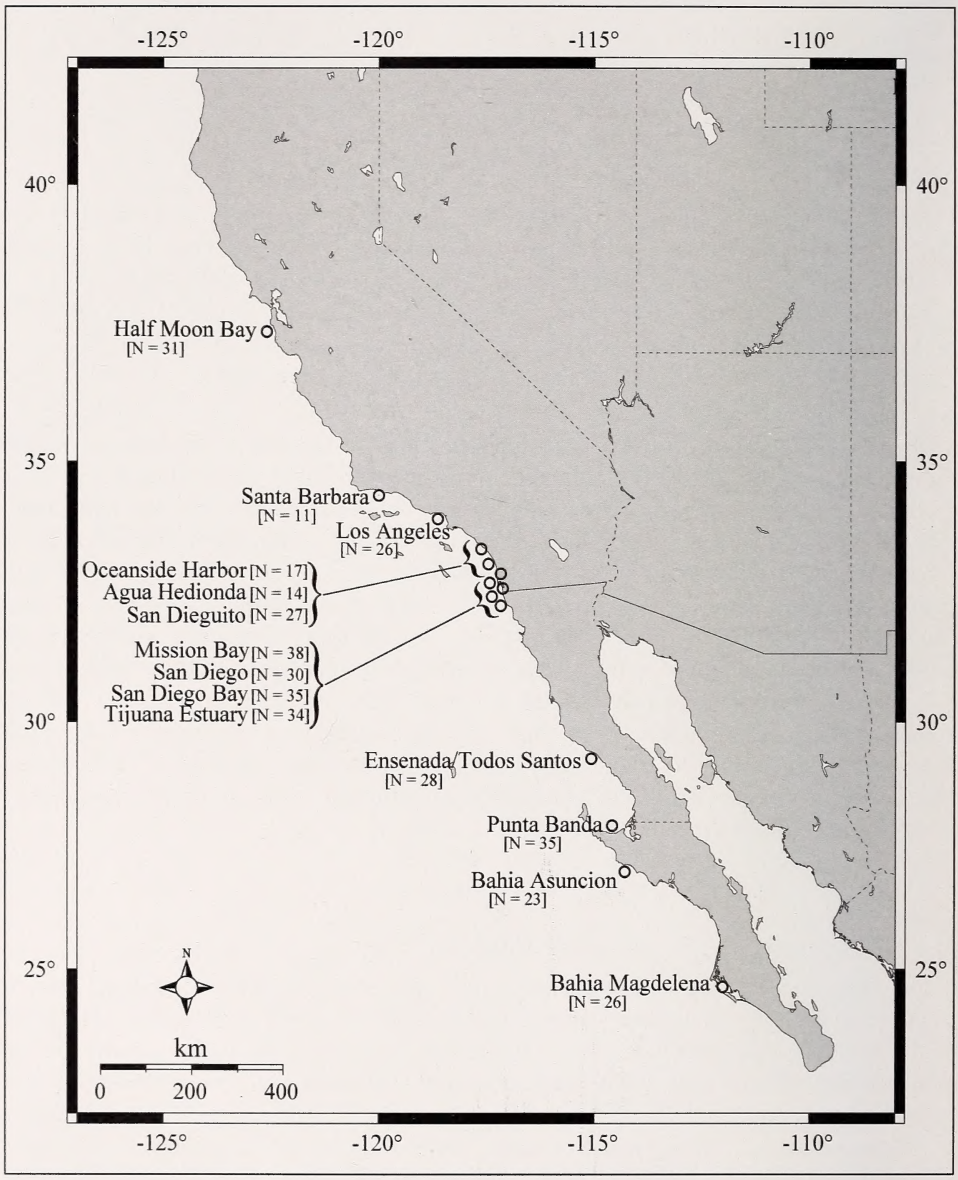

Fig. 1. *Paralichthys californicus.* Sampling locations and sample sizes for 375 individuals along the California coastline.

With the advent of the phylogeographic revolution in the late 1990's, many papers were written discussing the theoretical expectation of concordance between biogeographic boundaries and intra-specific, phylogeographical breaks (i.e., the concordance rule; see examples in Avise, 2000)). It was recognized that the genetic structure of a population may be influenced by a number of factors, including biogeographic barriers to dispersal (Bernardi, 2000; Bernardi, 2005; Blanchette and Gaines, 2007; Burton, 1998; Dawson, *et al.*, 2001), yet one assumption of the concordance rule that was not immediately recognized was that for a biogeographic boundary to function simultaneously as a

phylogeographic boundary, the expectation would be that sister species would exist on either side of the boundary due to the persistence of a common causal property of the geographic area restricting gene flow over evolutionary time scales. At that time, data from most studies highlighted the geographically similar locations of these phylogeographic and biogeographic breaks, particularly in the southeastern United States among marine organisms (e.g., Cape Canaveral, Florida). In coastal California, however, a pattern soon emerged in which geographical separations of marine faunal assemblages did not correlate with the geographic locations of phylogeographic breaks within species, and the generality of the "concordance rule" was challenged (e.g., Burton, 1998)

Further complicating the generality of California's hypothesized barrier was the realization that for some marine organisms, particularly those tied to aquatic inland habitats (i.e., estuaries and marshes), or with low dispersal potential (e.g., live-bearing fishes) a phylogeographic break was noted farther south in the Los Angeles region (LAR; Bernardi, 2000; Dawson, 2001; Dawson, *et al.*, 2002). Few studies to date have tested the functionality of either the LAR or CTZ in marine species with greater dispersal potential or vagility as adults, but notable examples include studies of rockfishes of the family Scorpaenidae (e.g., Hyde and Vetter, 2007; Hyde and Vetter, 2009).

The California Halibut (*Paralichthys californicus* Ayers 1859) is an ecologically and economically important flatfish species distributed from Washington State to southern Baja California with unsubstantiated records from the Gulf of California (R. N. Lea and R. Rosenblatt, pers. comm.). This range traverses the CTZ and the LAR. Contrary to early predictions, the California Halibut is known to utilize both embayments/estuaries and open coastal habitats for all stages of its life cycle (Fodrie, *et al.*, 2009). It is also a broadcast spawner with pelagic eggs and larvae. These characters provide an opportunity to examine the efficacy of the LAR and CTZ "barriers" for a species that is not restricted to aquatic inland habitats and that has higher dispersal potential than previous examples. Herein, we use mtDNA sequence data from the cytochrome *b* gene to examine the genetic architecture of California Halibut. We place these results within the context of recent and past genetic studies and show that California halibut provide yet another vexing example of the discordance between biogeographic and phylogeographic breaks in coastal California.

MATERIALS AND METHODS

Tissue samples from *P. californicus* were collected from 14 sites along the coast of California and Mexico throughout the entire effective range of the species (i.e., individuals are exceedingly rare North of San Francisco, California; Fig. 1). The northernmost site sampled was Half Moon Bay, while the southernmost site was Bahia Magdelena, Baja California Sur, Mexico. Samples were preserved in 100% ethyl alcohol and stored at room temperature.

Total genomic DNA was extracted using the DNeasy kit (Qiagen, Inc.) following manufacturer's protocol. Polymerase chain reaction (PCR) was initially performed using the primers (5′-GTGACTTGAAAAACCACCGTTG-3′) and (5′-AATAGGAAGTAT-CATTCGGGTTTGATG-3′), designed by Song *et al.* (1998) and Taberlet *et al.* (1992), respectively. Results were inconsistent with these primers, thus the species specific primers Para-CBF2 (5′- CTG ATG AAA CTT TGG CTC CCT -3′) and Para-CBR2 (5′- TAT GGG TGG AAG GGG ACT TTG TC - 3′) were designed which consistently amplified approximately 700 base pairs of the mitochondrial cytochrome *b* region. Twenty-five µl PCR reactions were prepared using BioMixRed (Bioline,USA) following manufacturer's

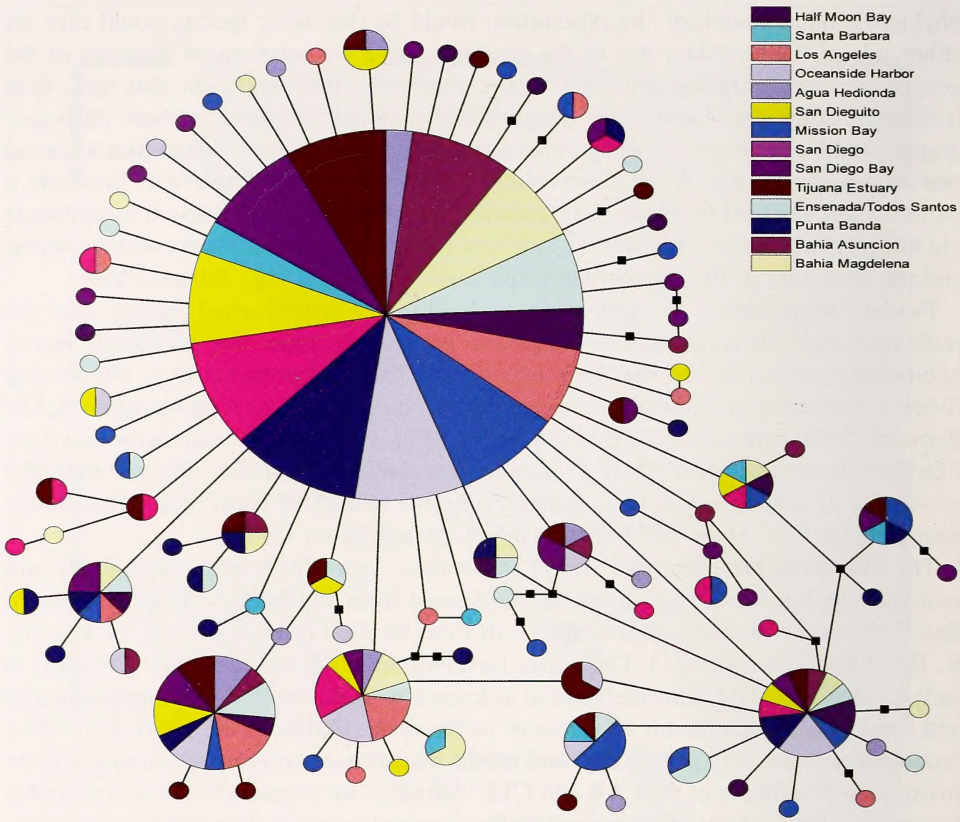

Fig. 2. *Paralichthys californicus.* Statistical parsimony network for 375 cytochrome *b* sequences. Small squares specify missing haplotypes; colors signify collection location. Circles are proportional to the number of individuals containing the haplotype with the smallest circles representing one individual.

protocols with the addition of 0.2 μM of each primer, and 10–100 ng DNA template. PCR amplifications were performed using the following cycling protocol: preliminary denaturing step for 2 min at 94°C, followed by 35 cycles of 30 s at 94°C, 45 s at 53°C, 45 s at 72°C, and a final continuous hold at 15 °C. Exonuclease I and shrimp alkaline phosphatase (ExoSAP) were used to eliminate non-incorporated oligonucleotide primers and excess dNTPs in successful amplification products. Direct sequencing of amplification products was performed in both directions using the PCR primers at the Hawai'i Institute of Marine Biology EPSCOR Sequencing Core Facility on an ABI3130 genetic analyzer.

Sequences were trimmed to a common length and collapsed to single stranded sequences using SEQUENCHER v. 4.1 (Sequencher® sequence analysis software, Gene Codes Corporation, Ann Arbor, MI USA), and aligned using CLUSTAL X (Larkin, *et al.*, 2007) with default settings. A statistical parsimony network of mtDNA haplotypes was created for *P. californicus* using the program TCS (Clement, *et al.*, 2000) under default settings (Fig. 2.). Hierarchical population structure was evaluated based on estimates of Φ_{st} for both the entire dataset and in a pairwise manner using ARLEQUIN (v. 3.11; Excoffier and Lisher, 2010). Values of haplotype and nucleotide diversity were obtained through ARLEQUIN. Departure from equilibrium conditions was assessed using Tajima's D and Fu's F_s (Table 2) as well as with mismatch distributions as calculated in ARLEQUIN. When

a unimodal distribution was found, we followed Li (1977) and Rogers and Harpending (1992), and fitted estimates of s, h_0 and h_1 to observed mismatch distributions to determine effective population sizes and time to coalescence. Coalescence analysis requires an estimate of generation time and rate of DNA evolution. Empirical values are not available for California halibut, so a range of values were used that bracket rates used in previous studies (Bowen, *et al.*, 2001). Mutation rates of 0.1–10% per million years within lineages and generation times of 1.5–10 yr were used.

A coalescence-based analysis of historical migration rates was performed using the program MIGRATE v. 3.1.6 (Beerli, 2009) to assess relative migration rates across the two hypothesized "barriers" (CTZ and LAR). The data were grouped into three pseudo-populations: North of Pt. Conception, Santa Barbara to the Tijuana Estuary, and Todos Santos to Bahia Magdalena. The Maximum Likelihood method was used under Markov Chain Monte Carlo (MCMC) search strategy of MIGRATE using default settings to estimate starting parameters for subsequent runs. A second MIGRATE analysis was performed using the estimates of Θ (N_e μ) and M (m/μ) from the first "run" as starting parameters. Estimates of Θ and M were within one order of magnitude and were thus accepted as good values following program documentation. Geographic distance between these pseudo-populations was not included in the analysis given the broad distances between individual sampling localities of the constituent members.

RESULTS

Overall, 681 base pair sequences of mtDNA cytochrome *b* were resolved for 375 individuals of *P. californicus*. Unique haplotypes were deposited in GenBank (JQ182307–JQ182398). Overall, there were 92 unique haplotypes found throughout all samples. San Diego Bay exhibited the highest number of unique haplotypes (N = 9) while Oceanside Harbor exhibited the least (N = 2). Overall nucleotide diversity was $\pi = 0.0026 \pm 0.0017$ and overall haplotype diversity was $h = 0.77 \pm 0.024$ (Table 1).

The statistical parsimony network showed a pattern consistent with the hypothesis that California Halibut represent a single, genetically homogeneous population with evenly dispersed haplotypes throughout the sampled range (Fig. 2). The fixation index (Φ_{st}) for the entire dataset was $\Phi_{st} = 0.0030$ ($p = 0.22$). In pairwise comparisons of the population, 5 out of 13 comparisons were statistically significant; however this significance was not apparent following Bonferroni correction for multiple comparisons (Table 2). Significant paiwise comparisons consistently included the open coast San Diego site. Tajima's D and Fu's F_s were negative and significant for nearly all sample locations and for the entire dataset (Table 1). Harpending's Ragedness index was $R = 0.01$ ($P = 0.98$; Fig 3).

Estimates of T, Θ_0 and Θ_1 are presented in Table 3. Estimated coalescence times did not vary depending on generation time (1.5–10yr) or mutation rate (0.1–10% per my). Coalescence times did vary, however, based on the mean, lower and upper limits of the estimated value of T (Table 3). The MIGRATE analysis indicated substantial effective migration among the three regions in a general North to South direction but not from South to North (Table 4).

DISCUSSION AND CONLCUSIONS

Point Conception has been a well-studied area due to its physical attributes and their implications for dispersal of marine organisms. Waters north of this region are characterized by strong, consistent upwelling and generally cooler surface waters, while those south of this region have weak, seasonal upwelling with relatively warmer surface

Table 1. *Paralichthys californicus.* Molecular diversity indices for 375 cytochrome *b* haplotypes. A single asterisk (*) indicates statistical significance at <0.05, double asterisk (**) indicates significance at <0.01.

Site	N	No. of Haplotypes	No. of Unique Haplotypes	Haplotype Diversity	Nucleotide Diversity	Tajima's D	Fu's F_s
California							
Half Moon Bay	17	11	5	0.8824 +/− 0.0718	0.002894 +/− 0.001925	−2.003*	−7.208**
Santa Barbara	11	7	3	0.8182 +/− 0.1191	0.002563 +/− 0.001816	−1.493	**−3.323****
Los Angeles	26	11	4	0.7785 +/− 0.0792	0.002548 +/− 0.001707	**−1.813***	**−5.633****
Oceanside Harbor	31	11	2	0.7269 +/− 0.0832	0.002078 +/− 0.001453	**−1.713***	**−6.167****
Agua Hedionda	14	10	5	0.9231 +/− 0.0604	0.003566 +/− 0.002307	−1.174	**−5.610****
San Dieguito	27	12	3	0.7350 +/− 0.0920	0.001991 +/− 0.001415	**−1.884***	**−8.713****
Mission Bay	38	19	8	0.8193 +/− 0.0621	0.003116 +/− 0.001972	**−2.251***	**−14.838****
San Diego	30	12	3	0.6805 +/− 0.0951	0.002093 +/− 0.001463	**−2.10***	**−7.805****
San Diego Bay	35	18	9	0.8185 +/− 0.0667	0.002833 +/− 0.001833	**−2.115***	**−14.841****
Mexico							
Tijuana Estuary	34	18	5	0.8093 +/− 0.0703	0.002947 +/− 0.001893	**−1.922***	**−14.662****
Ensenada/ Todos Santos	28	15	4	0.8201 +/− 0.0736	0.002785 +/− 0.001823	**−2.06***	**−11.162****
Punta Banda	35	16	6	0.7109 +/− 0.0869	0.002739 +/− 0.001786	**−2.287***	**−11.403****
Bahia Asuncion	23	9	3	0.5850 +/− 0.1222	0.001648 +/− 0.001242	**−2.269***	**−5.574****
Bahia Magdelena	26	12	4	0.7538 +/− 0.0900	0.002282 +/− 0.001569	**−2.099***	**−7.916****
All Samples	**375**	**92**	-			**−1.942***	**−8.918****

waters (Blanchette and Gaines, 2007; Diehl, *et al.*, 2007). Both the temperature difference and circulation patterns, along with discontinuities in hydrography, salinity, dissolved oxygen, and topography, suggest that marine organisms may experience restricted larval dispersal and thus increased potential for a decrease in gene flow Briggs, 1974; Seapy and Littler, 1980; Diehl, *et al.*, 2007). We found no evidence for a genetic break at Point Conception. Thus, it appears that none of the physical differences of this biogeographic boundary have affected the larval dispersal or gene flow of the California Halibut; instead they are best regarded as a single, genetically homogeneous population, at least over evolutionary time scales. These findings agree with numerous other studies examining the role of Point Conception in shaping the evolutionary history of marine organisms (Bernardi, 2000; Burton, 1998; Dawson, *et al.*, 2001; Lee and Boulding, 2007).

The California Halibut population was also continuous across the Los Angeles region (LAR). According to Dawson (2001), the LAR was fully or partially submerged before

Table 2. *Paralichthys californicus.* Population pairwise comparisons of Φ_{st} values of 375 cytochrome *b* sequences across 14 sample locations.

	Agua Hedionda	Half Moon Bay	Los Angeles	Mission Bay	Oceanside Harbor	San Deigo	San Dieguito	Santa Barbara	San Diego Bay	Bahia Asuncion	Bahia Magdelena	Ensenada/ Todos Santos	Tijuana Estuary	Punta Banda
Agua Hedionda	-	0.481	0.358	0.179	0.403	0.006*	0.230	0.395	0.155	0.072	0.029*	0.650	0.841	0.107
Half Moon Bay	−0.007	-	0.325	0.854	0.584	0.029*	0.391	0.767	0.538	0.312	0.234	0.952	0.727	0.799
Los Angeles	0.001	0.004	-	0.117	0.923	0.174	0.809	0.639	0.367	0.269	0.449	0.384	0.410	0.378
Mission Bay	0.014	−0.015	0.014	-	0.311	0.016*	0.091	0.916	0.288	0.125	0.069	0.745	0.393	0.295
Oceanside Harbor	0	−0.007	−0.018	0.003	-	0.059	0.662	0.521	0.344	0.288	0.381	0.862	0.721	0.437
San Diego	0.065*	0.030*	0.011	0.029*	0.020	-	0.199	0.299	0.327	0.458	0.690	0.011*	0.015*	0.063
San Dieguito	0.013	0.001	−0.015	0.016	−0.009	0.008	-	0.526	0.578	0.736	0.501	0.358	0.292	0.719
Santa Barbara	0.002	−0.018	−0.014	−0.028	−0.007	0.008	−0.006	-	0.775	0.431	0.705	0.519	0.605	0.814
San Diego Bay	0.018	−0.004	0.001	0.003	0.002	0.003	−0.004	−0.018	-	0.962	0.261	0.244	0.157	0.791
Bahia Asuncion	0.039	0.005	0.005	0.013	0.006	0	−0.011	0	−0.018	-	0.422	0.255	0.133	0.961
Bahia Magdelena	0.046*	0.010	0	0.018	0.001	−0.007	−0.002	−0.016	0.005	0	-	0.122	0.056	0.542
Ensenada/ Todos Santos	−0.012	−0.024	0	−0.008	−0.014	0.036*	0.001	−0.006	0.005	0.007	0.015	-	0.924	0.625
Tijuana Estuary	−0.022	−0.012	−0.002	0	−0.010	0.036*	0.004	−0.012	0.010	0.018	0.024	−0.014	-	0.204
Punta Banda	0.023	−0.013	0.001	0.003	−0.001	0.013	−0.007	−0.020	−0.007	−0.015	−0.003	−0.005	0.007	-

"*"indicates values are significant following Bonferroni correction. Values below diagonal are Φ_{st}, and above the diagonal are p values.

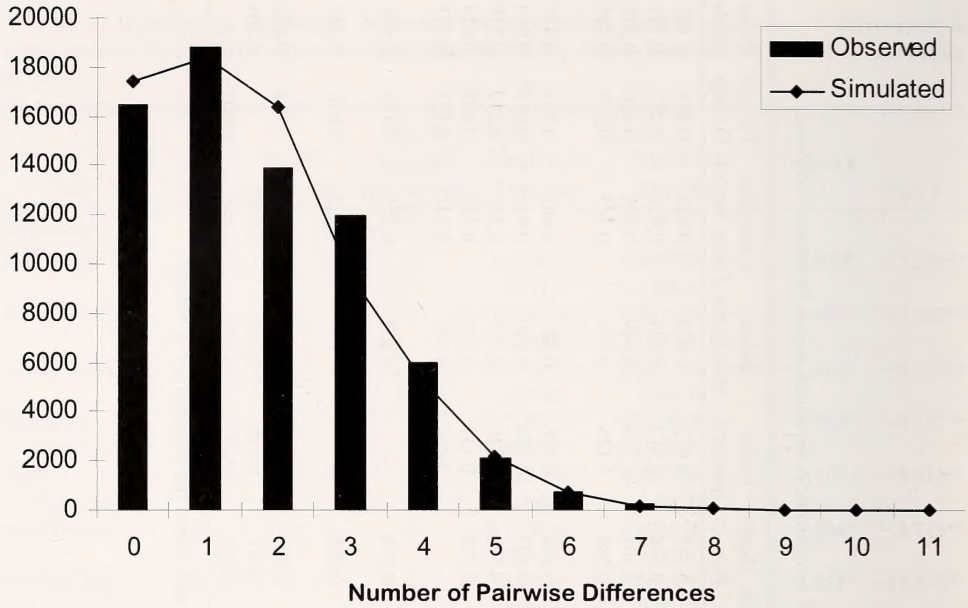

Fig. 3. Mismatch distribution for cytochrome *b* sequences of *Paralichthys californicus*. Harpending's "r" = 0.01 (P = 0.98).

the Late Pleistocene. Similar to the present day conditions, with a substantially-sized area submerged, there was an increase in shallow, coastal habitat available for marine organisms, particularly those that inhabit estuaries and bays. During the last ice age, the LAR subsequently emerged, leading to a significant loss of shallow coastal habitat. However given the complete loss of shallow coastal habitats elsewhere, the LAR may have provided glacial refuge given what little habitat remained in the LAR. This emergence most likely wiped out some coastal populations and created phylogeographic breaks in certain lineages (Ahnelt, *et al.*, 2004; Bernardi, 2005; Dawson, *et al.*, 2001; Dawson *et al.*, 2002), suggesting that historical fluctuations in sea level were likely key factors that contributed to these breaks (McGovern, *et al.*, 2010; Marko and Hart, 2011). Although populations of California Halibut may have been affected by this alteration in habitat across the LAR, we do not see evidence of a genetic break in the halibut population supporting this hypothesis. In addition, the estimated coalescence time for California Halibut of approximately 160,000 yr before present does not correlate with the last glacial cycle, an event that would have been recognized if populations were severely affected by the loss in habitat with the emergence of the LAR.

Table 3. Estimates of Tau (T), Theta naught (θo), Theta one (θ1), and Coalescence Times (CT; yr).

	Lower Bound	Mean	Upper Bound
T	0	2.175	5.262
θo	0	1.513	0.045
θ1	1.129	41215	Infinity
CT	13,656	159,691	330,837

Table 4. MIGRATE estimates of migrants (M) per generation, Θ, and likelihood scores (L). Top row indicates population from which migrants leave while left columns are recipient localities.

	L	Θ	North	Middle	South
North	1.993	0.0081	*	~0	31
Middle	1.993	0.0298	2920	*	~0
South	1.993	0.1154	2050	503	*

The MIGRATE analysis indicated that the three pseudopopulations were highly connected in a general North to South direction. This could represent longer-term gene flow over several thousand generations being affected by the general motion of the California Current. However, nearshore current fields, which may be those most expected to influence California halibut during their larval stage, are chaotic and generally do not echo the constant flow of the California current (Mitarai, *et al.*, 2009; White *et al.*, 2010).

Our results showed statistical pairwise differences of California Halibut in only the San Diego location. However, there are no obvious reasons for this phenomenon. For example, there are no differences in sizes or ages from the samples at San Diego which could suggest sampling a single cohort which may skew population signals and there are no geographic features which might be acting as a physical barrier.

The marine taxa that demonstrate phylogeographic structure in the LAR, mainly species of the family Gobiidae, share certain qualities that are susceptible to population bottlenecks during these periods, and these species tend to show deeper phylogeographic structure (e.g., they are egg layers, have low adult vagility and inhabit patchy supra-tidal or estuarine habitats, which presumably limits their dispersal capabilities). Halibut, however, have planktonic eggs and larvae, are more mobile as adults, and they also reside in continuous, sub-tidal habitats, factors that would suggest a refuge may not have been necessary or advantageous during Pleistocene sea level fluctuations and concomitant changes in habitat (Dawson, *et al.*, 2002). These differences in life history characteristics may explain why certain taxa show phylogeographic structure at LAR while others do not, including the California Halibut. In addition, other factors, including ecological parameters (e.g., kelp habitat and ocean circulation) may influence subtle genetic "patchiness" in California's marine species (Selkoe, *et al.*, 2010). The physical and biological factors mentioned above may thus work in concert with biological characteristics to design the genetic architecture of marine species in California.

Acknowledgements

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Abundance of the long-beaked common dolphin (*Delphinus capensis*) in California and western Baja California waters estimated from a 2009 ship-based line-transect survey

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Abstract.—The abundance of the long-beaked common dolphin (*Delphinus capensis*) is estimated from data collected during a 2009 ship-based line-transect survey. The survey was designed to provide fine-scale coverage of the known range of *D. capensis* along the California and west Baja California coasts. Estimates of *D. capensis* abundance presented are the highest to date for California waters and may reflect a combination of improved survey design for this species and increasing numbers of *D. capensis* in state waters. Estimates of *D. capensis* abundance within California waters are 183,396 (CV=0.41, 95% CI 78,149 – 379,325) animals. An additional 95,786 (CV=0.47, 95% CI 36,881 – 209,507) *D. capensis* were estimated in Baja California waters from the U.S./Mexico border south to the tip of Baja California. Total estimated abundance of *D. capensis* in California and Baja California west coast waters is 279,182 (CV=0.31, 95% CI 148,753 – 487,323) animals.

Introduction

In 2009, the Southwest Fisheries Science Center (SWFSC), a branch of the National Oceanic and Atmospheric Administration (NOAA), conducted a ship-based line-transect survey to estimate the abundance of long-beaked common dolphin (*Delphinus capensis*) in California waters and along the west coast of Baja California (Chivers *et al.* 2010). This was part of a larger mandate under the U.S. Marine Mammal Protection Act to collect data on marine mammal populations used to prepare marine mammal stock assessments published annually (Carretta et al. 2011). Surveys are conducted periodically to provide updates on marine mammal abundance and trends. Between 1991 and 2008, six coarse-scale vessel line-transect surveys were conducted along the U.S. west coast out to 300 nmi (Barlow 1995, Barlow 2003, Forney 2007, Barlow and Forney 2007, Barlow 2010). These surveys provided comprehensive estimates of abundance for short-beaked common dolphin (*Delphinus delphis*) in the California Current. However, transect coverage was not optimal for coastal species, such as *D. capensis*. Abundance estimates of *D. capensis* from previous coarse-scale surveys have been highly variable and characterized by small numbers of sightings and low statistical precision (Table 1). Part of this variability is because California waters represent the northern extent of the range of a *D. capensis* population which extends into Mexico. Gillnet bycatch of the California population of *D. capensis* has sometimes exceeded sustainable levels ("potential biological removal" or PBR) as defined under the Marine Mammal Protection Act (Wade and Angliss 1997). A lack of precise abundance estimates, in combination with human-caused mortality levels of this stock, prompted a more intensive, fine-scale survey of *D. capensis* coastal habitat in 2009 to provide improved estimates of abundance. Although this species also occurs in the Gulf of California, it was not practical to survey their entire range in 2009. Since

Table 1. Historic estimates of *D. capensis* abundance within California waters, from ship-based line-transect surveys. Multiple estimates in a given year reflect incorporation of new analysis methods to existing datasets, such as the use of covariates in line-transect analysis (Barlow and Forney 2007).

Survey year	Reference	*D. capensis* sightings (n)	Estimated abundance (CV)
1991	(Barlow 1995)	5	9,472 (0.68)
1991	(Barlow & Forney 2007)	5	16,714 (n/a)
1993	(Barlow & Forney 2007)	0	0
1996	(Barlow & Forney 2007)	6	49,431 (n/a)
2001	(Barlow 2003)	1	306 (1.02)
2001	(Barlow & Forney 2007)	2	20,076 (n/a)
2005	(Barlow & Forney 2007)	6	11,191 (n/a)
1991–2005 pooled	(Barlow & Forney 2007)	19	21,902 (0.50)
2005	(Forney 2007)	6	11,714 (0.99)
2008	(Barlow 2010)	7	62,447 (0.80)

management of the population is based only on abundance in U.S. waters and animals occur throughout their range year-round, the area surveyed in 2009 was adequate to assess the status of the U.S. population.

Field Methods

A ship-based line-transect survey was conducted in 2009 on the 62 m NOAA vessel *McArthur II* from September to December (Chivers *et al.* 2010). Transect coverage of the study area was designed to encompass the known range of *D. capensis* in California waters and along the west coast of Baja California, based on examination of historic (SWFSC) sightings (Figure 1A).

The survey design included approximately 4,800 km of transect lines, with different coverage goals for each of three 25-day sea legs (Figure 1B). Leg 1 effort targeted inshore

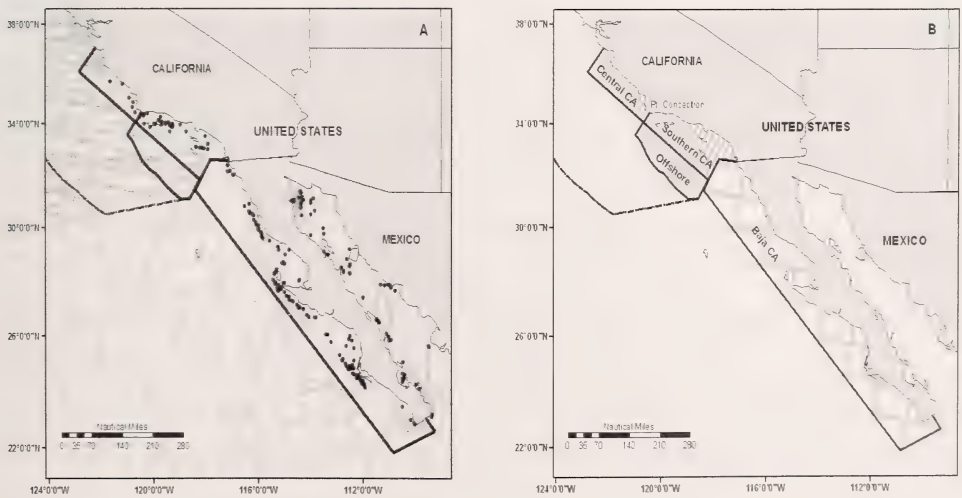

Fig. 1. (A) SWFSC ship survey line-transect effort and *Delphinus capensis* sightings prior to 2009. Solid black lines represent survey strata used to design transect coverage for the 2009 survey and dashed line represents a portion of the U.S. Exclusive Economic Zone (EEZ). Thin gray lines represent historic ship survey line-transect effort. (B) Planned transect coverage and geographic strata for the 2009 survey.

waters from Monterey Bay south to the U.S./Mexico border, with a series of 26 transects ranging from 40 to 170 km in length, up to 150 km offshore of the mainland. Leg 2 transects covered the waters of western Baja California, with a series of 15 transects in a saw-tooth pattern offshore to the shelf break, ranging from 85 to 195 km in length. Leg 3 transects included southern California transects from Leg 1, with additional offshore extensions of up to 250 km from the mainland. These additional offshore transects were not used to estimate abundance but were utilized to obtain additional data on stock structure of *D. delphis* in southern California offshore waters and to determine if the range of *D. capensis* was limited to inshore waters where it had been historically seen. Abundance and density were estimated for three strata: 'Central California', 'Southern California', and 'Baja California' (Figure 1). Areas for all strata were determined using ArcGIS 9.3 software, with a 'World Equal Area' map projection.

Line-transect methods were similar to previous SWFSC surveys described by Kinzey (2000) and Barlow and Forney (2007). The basic line-transect survey mode consisted of three experienced marine mammal observers searching from the flying bridge of the NOAA ship *McArthur II* at a height of 15.2 m above the water. Two observers searched port and starboard of the transect line using pedestal-mounted 25X binoculars, and a third observer acted as data recorder, searching the transect line primarily with naked eye and 7X binoculars. Surveys were conducted in 'closing mode' (Barlow and Forney 2007), whereby the ship diverts from the transect line to allow observers to better identify and count dolphin groups. Exceptions to closing mode occurred where navigational constraints prevented this or where closing mode made estimation of group size more difficult. For example, several dolphin groups (see Results) were too large and/or diffuse to effectively estimate group size in closing mode and therefore, passing mode was used. In passing mode, the ship maintains its course after animals are sighted and observers count animals as they pass on either side of the ship. Dolphin groups too large or diffuse to estimate group size in closing mode were known as 'mega-schools' and observers divided the task of estimating group size between the left and right sides of the ship as the ship passed through the school. Resulting group size estimates of 'mega-schools' represent the sum of estimates of two or more observers. Observers typically made three estimates of group size: a 'best', a 'high, and a 'low'. Only the observers' 'best' estimates were used in this study.

Observers aboard research vessels tend to underestimate dolphin group sizes because animals are diving and not available to be seen and because counting large groups of dolphins is a difficult task (Barlow *et al.* 1998, Gerrodette *et al.* 2002). Thus, estimates of group size require correction factors to address these biases. A NOAA Twin Otter aircraft was utilized during the 2009 survey to coordinate with the NOAA ship *McArthur II* to obtain digital aerial photographs of dolphin groups to calibrate observer estimates of group size. Photographs were taken using three Canon EOS-1 DS Mark III digital cameras mounted in the belly of the aircraft (Chivers *et al.* 2010). Digital aerial images of sufficient quality were obtained for 12 calibration groups (10 *D. capensis* and 2 *D. delphis*) where all six marine mammal observers aboard the *McArthur II* also obtained estimates of group size. Observer group size calibration coefficients were developed as described in the Analytical Methods section.

Analytical Methods

Standard line-transect methods were used to estimate the density and abundance of *D. capensis* and *D. delphis* (Buckland *et al.* 2001), using the program Distance 6.0

(Thomas *et al.* 2009). Only 'standard effort' transect data (effort on planned transect lines, excluding 'deadhead' effort between lines) where Beaufort sea state was between zero and 4, visibility was at least 3.5 nmi, and no fog or rain were recorded were used to estimate density and abundance. Dolphin density ($\hat{D}$) within a stratum was calculated as:

$$\hat{D}_i = \sum_{j=1}^{2} \frac{n_{i,j} \cdot f(0) \cdot S_{i,j}}{2 \cdot L_i \cdot g(0)_j} \quad (1)$$

where

$n_{i,j}$ = number of dolphin groups of size j detected in stratum i,
$f(0)$ = probability density function (km^{-1}) evaluated at zero perpendicular distance
$S_{i,j}$ = mean group size of dolphin groups of size category j in stratum i,
L_i = length of transect line (in km) surveyed in stratum i,
$g(0)_j$ = probability of detecting a dolphin group of size j on the transect line.

Values for $g(0)$ used in this analysis are based on those reported by Barlow and Forney (2007) for delphinid group sizes of ≤ 20 animals (0.856, CV=0.056) and > 20 animals (0.970, CV=0.017), respectively. Half-normal and uniform models with simple polynomial adjustment terms were fit to the perpendicular sighting distance data to estimate $f(0)$ and the effective strip width (ESW) for all geographic and group size strata pooled. The ESW is defined as that perpendicular distance from the transect line at which the number of objects detected beyond this distance equals the number missed within the same distance. Perpendicular sighting distances were right-truncated at 4.0 km (excluding 5–10% of the largest distances) to avoid fitting extreme values near the tail of the distribution. The model fit with the lowest Akaike's Information Criterion (AIC) was selected by the program Distance to estimate dolphin density. Because observers are less likely to detect small groups of dolphins at greater distances, this may introduce a positive bias into overall mean group size. The program Distance includes the option of correcting mean group size based on regressing the logarithm of observed group size versus perpendicular sighting distance. If the regression is significant at an alpha-level of 0.15, then the 'expected group size' based on the regression is used in place of the observed group size (Thomas *et al.* 2009). We implemented this Distance program option in our analysis. It should be noted that regression-based corrections to mean group size address the bias that observers are more likely to miss small groups. This is independent of observer calibrations from aerial photographs used to correct the bias of undercounting of detected groups, which we discuss below.

Total abundance was estimated as the sum for all three geographic strata (Central California, Southern California, and Baja California) as:

$$\hat{N}_i = \sum_{i}^{3} \hat{D}_i \cdot A_i \quad (2)$$

where $\hat{N}_i$ is estimated abundance in stratum i and A_i is the area of the stratum. Encounter rate (n/L) variance was estimated empirically within the program Distance from the individual survey effort segments. We tested a range of effort segment lengths as sampling units (5 km to 100 km), to see if resulting coefficients of variation (CV) in abundance

estimates were significantly affected by segment length choice. An initial sensitivity analysis suggested that segment lengths of 20 km provided the greatest precision for this particular dataset (in exploratory analyses, CVs for all strata combined ranged from 0.43 to 0.51 using segment lengths of 5 to 100 km). Within a stratum i, the CV of the abundance estimate for groups of size j was calculated as the square root of the sum of the squared CVs of the parameters group size, encounter rate, detection function, and trackline sighting probability:

$$CV(\hat{N}_{i,j}) = \sqrt{CV^2(S_{i,j}) + CV^2(\frac{n_{i,j}}{L_i}) + CV^2(f(0)) + CV^2(g(0)_j)} \quad (3)$$

The variance and CV of the combined abundance (across all group size categories j within stratum i) was calculated as:

$$Var(\hat{N}_i) = \sum_{j=1}^{2} (CV(N_{i,j}) \cdot N_{i,j})^2 \quad (4)$$

and

$$CV(\hat{N}_i) = \frac{\sqrt{Var(\hat{N}_i)}}{\hat{N}_i} \quad (5)$$

Variances for combined estimates of abundance (multiple strata) were also calculated as shown in Equation 5. Ninety-five percent confidence intervals for abundance estimates were estimated by simulating a log-normal distribution from each point estimate and associated CV and taking the 2.5^{th} and 97.5^{th} percentiles respectively, as the lower and upper limits of the confidence interval.

Group size calibration

Group size calibration coefficients were developed from digital aerial photographs of 12 dolphin groups (10 *Delphinus capensis* and 2 *Delphinus delphis*) and corresponding observer 'best' estimates of group size from the research vessel. Three counters independently counted dolphin numbers from aerial photographs of the 12 calibration groups and the 'true group size' for each sighting was calculated as the mean of the three photo counts (Table 2). We calculated individual observer calibration coefficients by fitting a log-transformed, linear regression (intercept = 0) to the 12 photo calibration groups and 'best' estimates of group size. The calibration coefficient, β_0, for a given observer is:

$$\ln \bar{S}_{best} = \beta_0 \cdot \ln S_{photo} \quad (4)$$

where

S_{best} = the observer's best estimate of group size

and

$\bar{S}_{photo}$ = mean 'true group size' determined from aerial photographs.

Estimates of group size for individual observers were corrected as follows:

$$\ln S_{corrected} = \ln S_{best} / \beta_0 \quad (5)$$

In cases where multiple observers estimated separate portions of a mega-school, a single

Table 2. Dolphin counts from digital aerial photographs of 12 *Delphinus* groups obtained in 2009 and used for group size calibration. Uncorrected field estimates of mean group size and corrected estimates of group size, based on 2009 and ETP calibration coefficients are shown.

Sighting Number	Species	Mean Photo Count	Uncorrected Mean Best Estimate	Corrected Mean Best Estimate (2009 coefficients)	Corrected Mean Estimate (ETP correction factor)
161	*D. capensis*	569	310	590	360
290	*D. delphis*	272	155	269	180
291	*D. capensis*	634	353	681	411
292	*D. capensis*	1394	396	778	461
293	*D. capensis*	776	283	530	329
320	*D. capensis*	48	33	46	39
322	*D. capensis*	35	20	27	23
512	*D. capensis*	475	613	1166	713
514	*D. capensis*	284	289	561	336
526	*D. capensis*	1281	404	795	470
528	*D. capensis*	574	303	553	352
705	*D. delphis*	122	159	278	185

calibration coefficient was used and calculated as the mean of all individual observer calibration coefficients. For comparison, we also report estimates of abundance obtained using uncorrected group sizes (calibration coefficients = 1.00) and those obtained by applying a mean group size correction factor for 52 observers calibrated during line-transect surveys in the Eastern Tropical Pacific (ETP) (Gerrodette *et al.* 2002, Gerrodette and Forcada 2005). The ETP correction factor is based on the mean ratio of observer best estimates to photo counts (0.860), with a mean of 38 calibration groups per observer (Gerrodette *et al.* 2002, Gerrodette and Forcada 2005). Estimates of dolphin density and abundance presented in the Results section utilize the calibration coefficients developed from 12 calibration schools photographed in 2009.

Results

Over 5,000 km of standard line-transect effort was conducted during the 2009 survey in Beaufort sea states 0 through 5 (Table 3; Figure 2). The length of completed transects slightly exceeds the length of the designed transect grid because Southern California stratum transects were surveyed on both Legs 1 and 3. Standard effort sightings included 88 groups of *D. capensis* (Figure 3). The observed distribution of *D. capensis* sightings in 2009 did not differ appreciably from historic sighting distributions (Figures 1 and 3). No sightings of *D. capensis* were made in the Offshore stratum, though some groups were sighted near the boundary of the Offshore and Southern California strata. Observers underestimated group size for the 12 calibration schools, as evidenced by the mean ratio of observer best estimates to aerial photo counts (=0.669, Table 2). Four out of six observers had group size correction coefficients of less than one and the degree of underestimation increased with group size (Tables 2 and 4; Figure 4). After correcting observer best estimates with linear regression, the mean ratio of corrected counts to aerial photo counts was 1.20 (Table 2). A half-normal model provided the best fit to the perpendicular distance data over competing uniform models, based on the lowest AIC values (Figure 5). The mean ESW for *D. capensis* was 2.81 km (CV=0.13), which is similar to previous estimates reported by Barlow and Forney (2007) and Barlow (2010), who reported values of 2.85 km and 2.62 km, respectively.

Table 3. Stratum sizes and length of transect lines surveyed during standard survey effort. Estimates of density and abundance in this report do not include survey effort and sightings within the 'Offshore' stratum.

Stratum	Study Area (km^2)	Length of transects surveyed (km)			
		Beaufort 0–3	Beaufort 4	Beaufort 5	Total (Beaufort 0–5)
Central California	23,259	233	82	68	383
Southern California	42,263	1,059	740	340	2,139
Offshore	32,094	291	292	180	763
Baja California	175,493	580	1,016	142	1,738
TOTAL	273,109	2,163	2,130	730	5,023

Mean group size of *D. capensis* (corrected for undercounting bias) was 454 animals (Table 5). This is larger than that reported by Barlow and Forney (2007), who reported a mean group size of 315 animals, but smaller than the mean of 535 animals recently reported by Barlow (2010) from a 2008 survey. Approximately 279,000 *D. capensis* were estimated for all geographic strata combined, with approximately 180,000 animals in U.S.

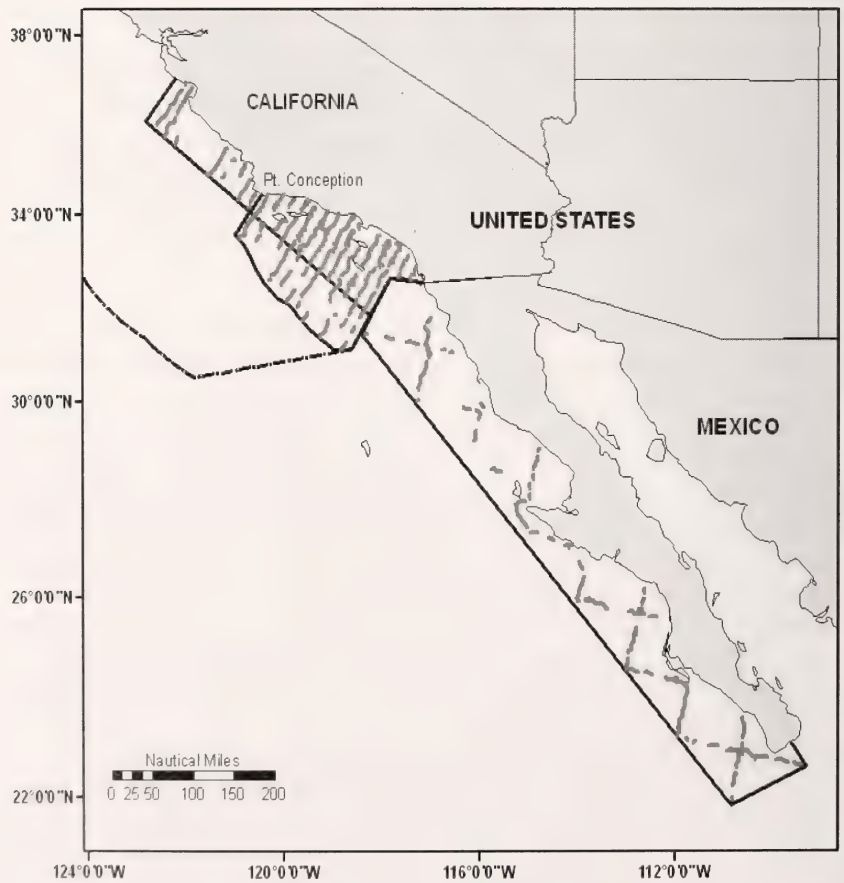

Fig. 2. All standard survey effort completed during Legs 1–3 (07 September – 09 December 2009).

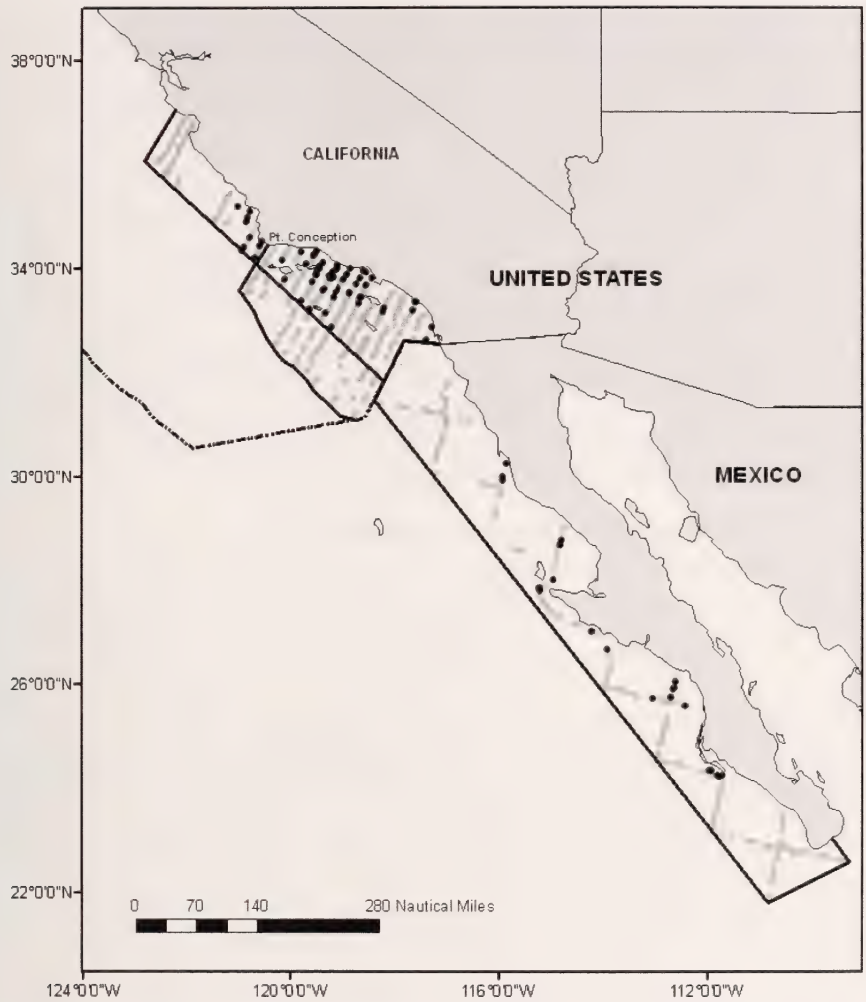

Fig. 3. Sighting locations of long-beaked common dolphin (*D. capensis*, n=88) during standard survey effort (gray lines).

west coast waters (Table 6). These estimates are based on using observer calibration coefficients calculated from 12 *Delphinus* groups photographed in 2009. Corrected estimates were on average, nearly double that of estimates not corrected for underestimation of group size (Figure 6). Estimates of density and abundance for *D. capensis* are provided in Table 6.

Discussion

Estimated abundance of *D. capensis* in California waters in 2009 (≈ 180,000 animals) is the highest of any ship line-transect survey to date. Nearly 40% of the estimate (≈ 70,000) comes from the Central California stratum, where relative survey effort was low, group sizes were large, and precision of the estimate was poor (CV=0.79). The ratio of *D. capensis* to *D. delphis* sightings during standard transect effort was nearly 1:1 (88 and 90 sightings, respectively) within our strata. Previous SWFSC line-transect surveys from 1986–2008 within the same strata had a ratio of 1:3.6 (73 and 262 standard-effort

Table 4. Individual group size correction coefficients based on 'best' estimates of group size for 12 calibration groups photographed in 2009.

Observer	Group size correction coefficient (2009)
A	0.859
B	0.943
C	0.874
D	0.909
E	0.880
F	0.931
Mega-school aggregate	0.900

sightings, respectively) *D. capensis* to *D. delphis* sightings (SWFSC unpublished data). The difference in relative sighting numbers of each species may reflect differences between fine-scale and coarse-scale transect coverage between previous surveys and ours, but it may also reflect increasing trends in abundance of *D. capensis*.

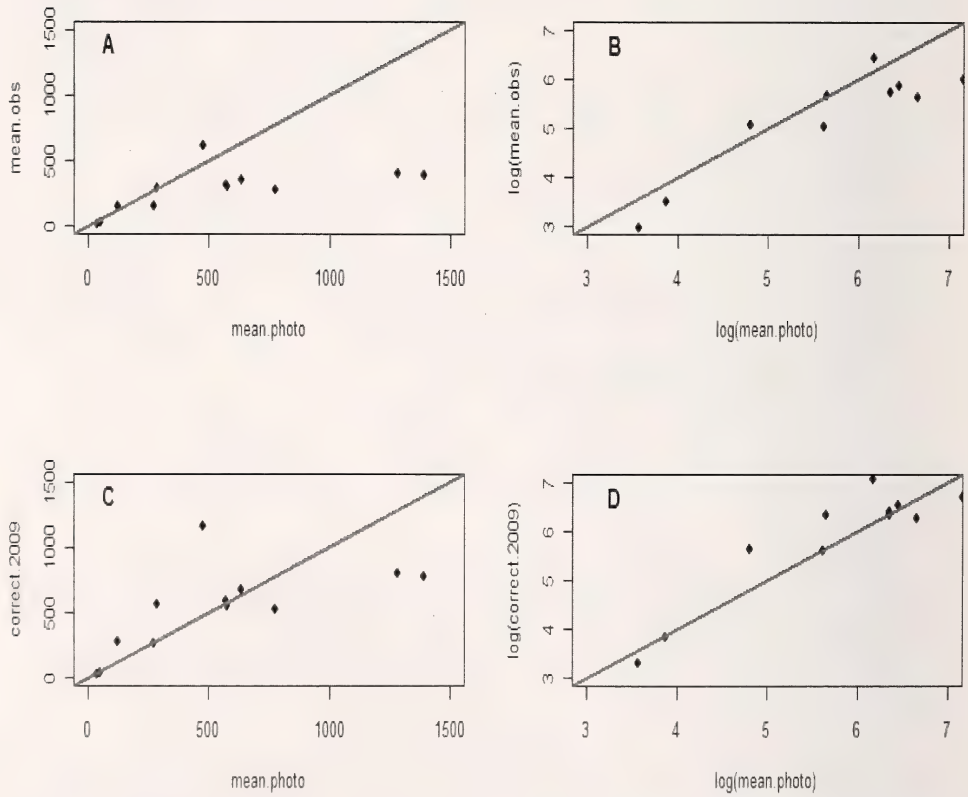

Fig. 4. Top Row: Mean photo counts and mean observer estimates (mean of six 'best' observer estimates) for 12 calibration groups of common dolphin photographed during 2009. Both raw (A) and log-transformed values (B) are shown. Bottom row: Corrected observer estimates based on the linear relationship between observer estimates and 'true group size' from aerial photographs. Both raw (C) and log-transformed (D) values are shown. Diagonal lines represent a 1:1 relationship between uncorrected/corrected observer estimates and counts from aerial photographs. In the absence of estimation error, all points would fall on the diagonal line.

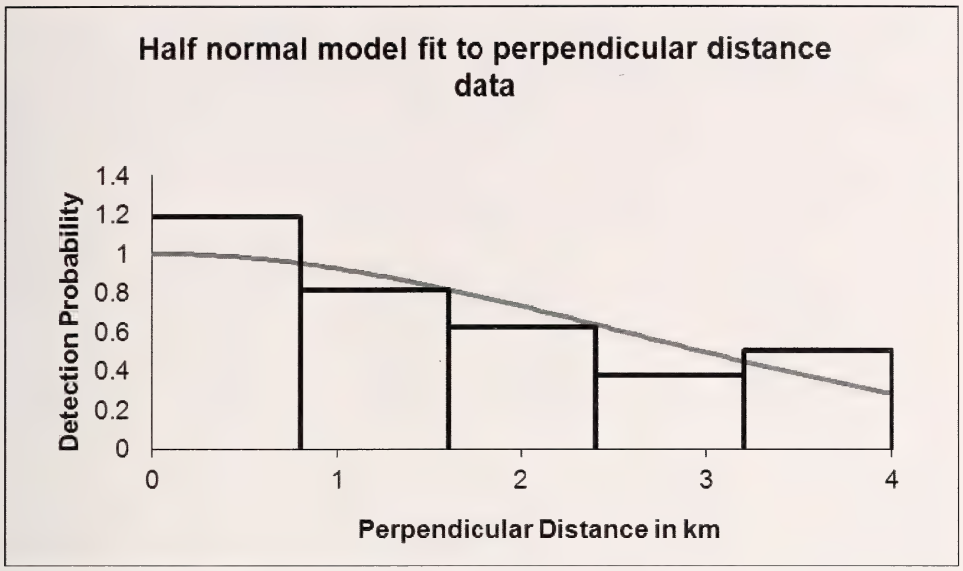

Fig. 5. Half normal model fit to *D. capensis* perpendicular sighting distances (n=56) for Beaufort sea states 0 to 4 and visibility ≥ 3.5 nmi. Model fit statistics are $f(0)=0.356$ km^{-1}, CV=0.13, chi-square $p=0.445$, and the effective strip width (ESW) is 2.81 km. Truncation distance is 4.0 km.

The ratio of *D. capensis* to *D. delphis* strandings in southern California increased following a strong 1982–83 El Niño (Heyning and Perrin 1994). Within San Diego County, dramatic increases in the ratio of *D. capensis* to *D. delphis* strandings were observed from 2006–2008 (Danil *et al.* 2010) and these have persisted through 2010 (SWFSC unpublished stranding data). Trends in *D. capensis* abundance are not apparent from a series of six line-transect cruises conducted by SWFSC between 1991 and 2008, but it is notable that the most recent survey in the series (2008) yielded the highest estimate of abundance (≈ 62,000 animals, Barlow (2010), Table 1). An abundance trend analysis for *D. capensis* would be difficult to perform, as the line-transect estimates are based on few sightings and inter-annual oceanographic variability likely influences the distribution of this trans-boundary population. Discerning a trend is also confounded by the fairly recent recognition of *D. capensis* as a separate species (Heyning and Perrin 1994) and the related issue that marine mammal observers may have experienced a 'learning curve' in their ability differentiate *D. capensis* from *D. delphis* since that time. The relatively high estimate of *D. capensis* abundance in 2009 may be related to a

Table 5. Number of standard-effort sightings (*n*) of *D. capensis* and mean group sizes (based on 2009 photographic calibration coefficients) for three geographic strata where density and abundance were estimated. Only groups used for density and abundance estimation are included in this table. Mean group size for all strata is calculated as the weighted mean (by number of sightings in each strata) for all three strata.

	Central California		Southern California		Baja California		All Strata	
Species	*n*	Mean group size	*n*	Mean group size	*n*	Mean group size	*n*	Mean group size
Delphinus capensis	6	716.0	36	481.3	14	274.3	56	455

Table 6. Total number of sightings (n), estimated abundance (N), coefficients of variation (CV), lower and upper 95% confidence intervals by strata for long-beaked common dolphins. Estimates are based on group size calibration coefficients estimated from aerial photographs obtained in 2009 (see text). Stratum estimates for 'Southern CA' represent pooled estimates of Leg 1 and Leg 3 survey data. U.S. EEZ stratum values represent combined Central CA and Southern CA estimates, but do not include sightings and effort data from the 'Offshore' stratum in Figure 1. No sightings of long-beaked common dolphin were recorded in the Offshore stratum.

Delphinus capensis	Stratum	n	N (CV)	Lower 95% CI	Upper 95% CI	Density per 1000 km^2
	Central CA	6	71,658 (0.79)	14,650	224,313	3,080
	Southern CA	36	111,738 (0.44)	44,618	229,417	2,643
	Baja CA	14	95,786 (0.47)	36,150	205,078	545
	U.S. Strata	42	183,396 (0.41)	78,149	379,325	2,798
	All strata	56	279,182 (0.31)	148,753	487,323	1,158

moderate El Niño event that began in mid-2009 (NOAA Climate Prediction Center), which may have shifted *D. capensis* distribution northward into U.S. waters. Differences in abundance estimates between this and previous surveys may also be due to analytical differences. We did not use Beaufort 5 data in our analysis, which has been necessary to include in previous survey analyses that suffered from poor weather. Nor did we use covariate modeling in our line-transect approach (Marques and Buckland 2003, Barlow and Forney 2007), but instead utilized simple stratification to select good weather conditions for inclusion (which was only possible because of the inshore nature of our transect coverage).

Our estimates are also influenced by the group size correction factors derived from the aerial photographs, though it should be noted that even our uncorrected estimates of abundance are higher than any previous estimates in this region (Table 1, Figure 6.).

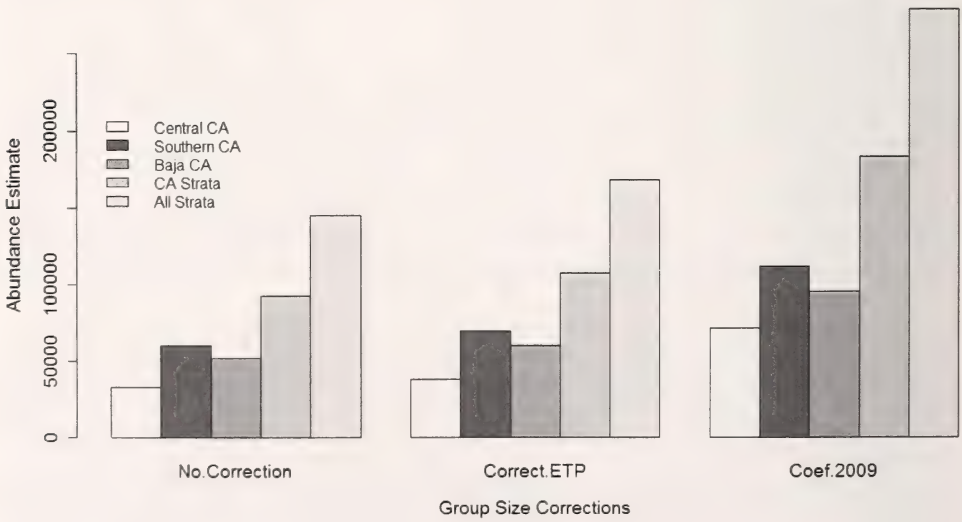

Fig. 6. Estimates of abundance by stratum for long-beaked common dolphin (*Delphinus capensis*). Estimates shown are based on uncorrected group sizes, group size corrections based on coefficients developed from 2009 aerial photographs, and a global correction factor for 52 observers, based on the ratio of observer best estimates to photo counts in the Eastern Tropical Pacific (Gerrodette *et al.* 2002).

Abundance estimates obtained with group size calibration coefficients based on 2009 aerial photographs were nearly double that of abundance estimates obtained with uncorrected group sizes (Figure 6). This is similar to the ratio of mean photo counts divided by mean observer counts (1.87) for the 12 calibration groups in Table 2. This highlights the challenges of accurately estimating dolphin numbers from a research vessel. The 2009 coefficients also provided estimates that are considerably higher than estimates that would be obtained if one applied the inverse of the mean ratio of observer best estimates to aerial photo counts (=0.860) for 52 calibrated observers in the ETP (Gerrodette *et al.* 2002) (Figure 6). The ETP correction factor is based primarily on spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphin schools, where the mean number of dolphins per school was approximately 230 (based on photo counts). In contrast, our calibration coefficients are derived from 10 schools of long-beaked common dolphin and 2 schools of short-beaked common, with a mean of 539 animals per school (Table 2). Long-beaked common dolphin schools are typically characterized by the largest group sizes of any cetacean encountered in the California Current (Barlow and Forney 2007). Barlow and Forney (2007) noted that in their calibration of observers' estimates of group size, it was apparent that proportionately larger corrections were applied to larger groups. Thus, the large increases in group size (and abundance) resulting from our calibrations are not extraordinary, considering the relatively large mean group sizes observed in 2009.

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Commercial fishery effort for California spiny lobster (*Panulirus interruptus*) off Orange County, California before State Marine Reserve implementation

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Abstract.—The California spiny lobster (*Panulirus interruptus*) commercial fishing effort along the southern Orange County, California coastline was examined using fishery-independent counts of trap marker buoys and fishery-dependent information submitted to the California Department of Fish and Game in the required commercial logbooks. Buoy counts were conducted in spatially-discrete subsections of the coastline inshore of the 30-m isobath to determine the density of fishing effort at a scale finer than is afforded by the standard fishing blocks used by the Department of Fish and Game. Both the buoy densities and fisherman-reported trap pull counts recorded declining effort across the area as the season progressed. Effort was more diffuse at the beginning of the season, but increasingly focused on areas covered by giant kelp canopy, including the boundary of a previously existing, small no-take marine reserve located in the study area. General effort declined as the frequency of capturing a harvestable California spiny lobster declined. The catch per unit effort of harvestable and sublegal individuals was found to decline at highly correlated rates with no effect on the following season. Fishing regulations in portions of this study area will be increased through the implementation of a network of no-take marine reserves. Data presented herein provides a baseline to compare future fishing effort in the Laguna Beach area after two of the three most intensively fished sites are closed due to their inclusion in the Laguna Beach State Marine Reserve and adjoining State Marine Conservation Area.

Introduction

The Orange County coastline between Huntington Beach and Doheny State Beach, California is characterized by cliff-backed sandy beaches interspersed between numerous headlands, where rocky intertidal substrate extends offshore as subtidal reefs. As a result of the extensive rocky habitat, the area is targeted by the commercial California spiny lobster (lobster; *Panulirus interruptus*) trap fishery except in the no-take Heisler Park State Marine Reserve (HPSMR) located off the Laguna coast (McArdle 1997; OCMPAC[1]). In the Orange County area, lobster traps are typically deployed from small boats around shallow reefs and hard structure with holes and crevices where lobsters conceal themselves during the day (Mitchell et al. 1969). California Department

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[1] Orange County Marine Protected Areas Committee. 2009. MPA sites and regulations. http://www.ocmarineprotection.org/mpa_sites_and_regulations.php. Accessed 17 April 2009.

of Fish and Game designated October to March each year as the commercial lobster fishing season (Barsky 2001), with most landings historically recorded during the first month of the season (Parnell et al. 2007; CDFG 2008). California commercial fishery regulations require each trap be attached individually to a buoy marked with the owner's commercial fishing license number, followed by a "P" for commercial lobster pot to make their identification easier (CDFG 2011). After the first Tuesday in October, or nearly one week after the season opens on first October Wednesday, buoys may be submerged by a timed release device called a pop-up.

Harvest effort has been routinely recorded for the commercial fishery through logbooks (CDFG 2011). The commercial logbooks record the number of traps retrieved (pulled) and the number of lobsters taken, but they do not provide fine-scale spatial information on the location of the trap set. Rather, harvest sites are designated within California Department of Fish and Game fishing blocks, which are predesignated 10 min latitude × 10 min longitude areas, although blocks along the coastline are often not square and therefore of smaller and variying size. At this spatial resolution, the fishing effort along gradients inside and outside a marine protected area (MPA) cannot be fully evaluated. Therefore, we attempted to evaluate the level of fishing effort along the Orange County coastline, including the area surrounding the HPSMR, which will be subsumed into future lobster no-take marine reserves; a complex including the adjoining Laguna Beach State Marine Reserve and State Marine Conservation Area[2]. Basic information at a spatial scale finer than the California Department of Fish and Game fishing blocks will be needed to evaluate the impacts of the newly designated MPA complex. Of specific interest is the responses in the lobster aggregations that will be released from harvest pressure within the new MPA complex. We expect areas open to fishing effort would likely receive pressures proportional to their production of havestable (>83 mm carapace length) individuals. The presence of a no-take reserve within the area during the survey may provide insights into what future effort can be expected once the new no-take marine reserves have been implemented. We attempt to address this by first describing the present baseline effort under existing spatial management regulations prior to the implementation of the MPA complex.

Materials and Methods

Fishing pressure was estimated by counting commercial lobster fishing trap buoys as a proxy for each individual trap during the 2008–2009 commercial fishing season (1 October 2008 to 18 March 2009). Counts were conducted monthly (except February 2009) from a small vessel between 3 October 2008 and 6 March 2009 by two observers under clear skies and calm seas between 0600 and 1100 h. Final counts represent the mean of the two counts. The use of pop-ups on buoys could not be quantified, but we assumed its impact on the counts would likely be most pronounced between the first survey, completed before pop-ups were allowed, and the second survey after pop-ups were allowed. In either case, these buoy counts represent a conservative estimate of fishing effort as the number of submerged buoys could not be verified.

Surveys were completed within three California Department of Fish and Game fishing blocks (737, 738, and 757; Figure 1). These fishing blocks (block) encompassed

[2] California Fish and Game Commission gives final approval for south coast marine protected areas. http://www.dfg.ca.gov/news/news10/2010121501-Commission-Approves-SCMPA.html. Accessed, July 15, 2011.

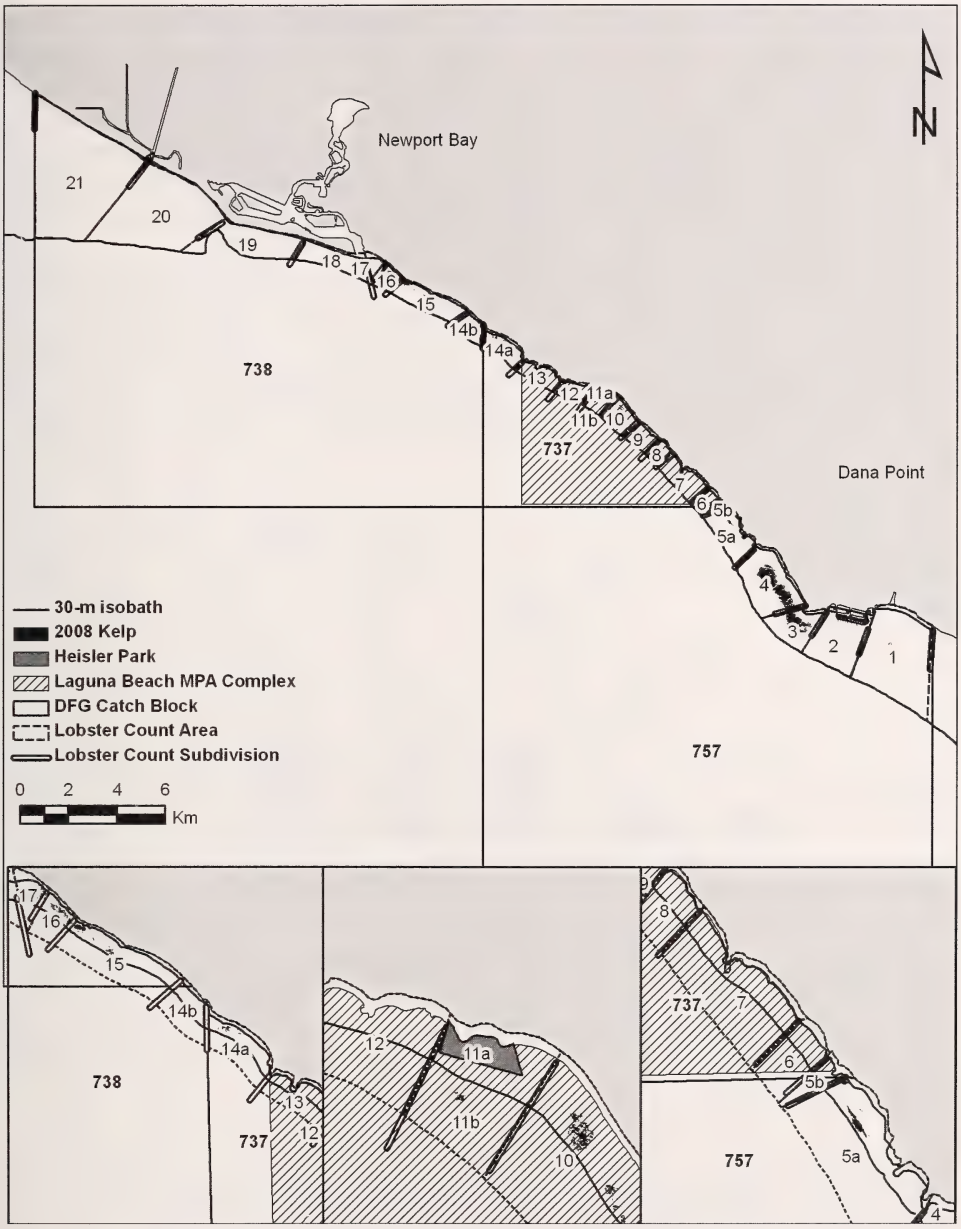

Fig. 1. Map of the study area including all three catch blocks (757, 738, and 737) and the subsections delineated for the current study, Heisler Park no-take marine reserve (11a), and the Laguna Beach MPA complex that includes the Laguna Beach State Marine Reserve and the Laguna Beach State Marine Conservation Area. The occurrence and spatial distribution of the giant kelp canopy mapped during aerial surveys in 2008 are also depicted.

approximately 62 km of linear coastline. Each block was further subdivided into subsections designated by landmarks easily recognized from the deck of the survey vessel with an offshore extent bounded by the 30-m isobath (Figure 1). The HPSMR is within block 737 designated subsection 11a. Areas (km^2) of each subsection were calculated

using ArcMAP[3]. The trap density (count/km^2) was calculated for each subsection from the monthly counts. Similar density estimates were calculated by block to better summarize the surveys at a more comparable spatial scale to the commercial fishery records. It should be noted, however, that only a subset of the area of each block was surveyed as the blocks extended offshore beyond the 30-m isobaths. No information was collected on buoys, if present, located offshore of the 30-m isobaths. The rate of declining effort was measured as the percent of the October buoy density observed each subsequent month of the season.

Habitat information was described using giant kelp (*Macrocystis pyrifera*) maximum annual canopy area as a proxy of hard substrate within each subsection. Giant kelp canopy areas surveyed in December 2008 were compiled from MBC (2009[4]) with the subsection areas calculated in ArcMAP. Confirmation of the co-occurrence of giant kelp canopy and hard substrate was done by reviewing habitat maps in Marinemap[5]. Spearman rank correlation was used to compare the giant kelp canopy area by subsection with survey-specific buoy densities.

The CDFG provided commercial lobster fishery logbook data (2000–2009) summarized by month and fishing block on the number of traps pulled, legal individuals retained and sublegal individuals returned. Due to fishermen confidentiality requirements, data were only provided for blocks where at least three fishermen set traps that month (K. Barsky, pers. comm[6].). We examined these data for long-term trends in effort. Despite the spatial scale differences, the commercial landing data were used as an independent verification of the buoy density estimates. Linear regression was used to compare the monthly buoy count densities by block (737, 738, and 757) against the corresponding trap pull records for the 2008 commercial season. The mean catch rate ($\pm$ standard error), or catch per unit effort (CPUE; count/trap) was calculated for the entire survey area, after combing blocks, for each of the 2000 to 2009 commercial seasons. A one-way ANOVA with SNK multiple comparison test was used to compare the October CPUEs for each commercial season for legal-sized individuals to test for changes in harvest success. Fisherman response to declining catches was evaluated by regressing the legal-sized CPUE against the number of traps pulled for each month in the 2008 season when concurrent buoy counts were completed. Linear regression was used to compare the legal and sublegal CPUEs for each block by season, 2000–2009, to examine for similarities in their trends over the season. All statistical analyses were completed using Sigmaplot 11 (SYSTAT[7]).

Results

Five monthly (minus February) counts of commercial lobster trap buoys were made during the 2008–2009 California lobster fishery season. A total of 8676 buoys were counted during the five surveys in each of the three fishing blocks. Total buoy density

[3] ESRI 2010. ArcMap Geographic Information System software version 10. ESRI, Redlands, California.

[4] MBC Applied Environmental Sciences. 2009. Status of the Kelp Beds 2008 San Diego and Orange Counties. Prepared for the Region Nine Kelp Consortium.

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[6] K. Barsky, Senior Invertebrate Specialist, California Department of Fish and Game, Ventura, California

[7] SigmaPlot version 11. Systat Software, Inc. San Jose, California.

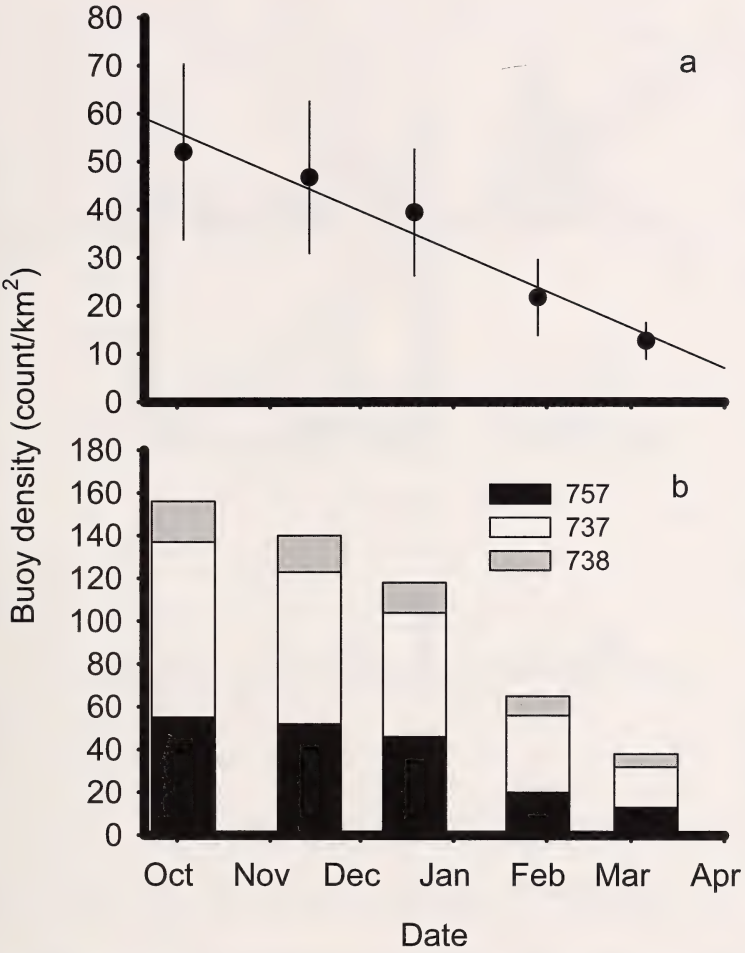

Fig. 2. a) California spiny lobster trap marker buoy density (± standard error) summed across all three fishing blocks by survey date during the 2008–2009 commercial fishing season and the best fit linear regression ($R^2 = 0.94$) describing the general trend, b) total buoy density in each fishing block depicted in Figure 1 by survey date.

linearly ($R^2 = 0.94$, $p = 0.006$) declined each month of the season (Figure 2a). Effort was greatest in block 737 where 51% of the total buoy density was observed, after standardizing for the area surveyed. This was followed by block 757 with 36% and block 738 with 13%. Effort in block 757 was initially the most consistent registering the smallest change between the first and second survey while the remaining block-specific densities declined each month (Figure 2b). Block 757 densities registered the largest month-month decline with 48% fewer buoys observed between the December and January surveys, as compared to the October baseline.

The subsection densities revealed distinct variations in effort within each block (Figure 3). Subsections 3, 9, and 11b were among the most intensively fished subsections. These include relatively unique areas, in comparison to the rest of the survey area, including the headlands of Dana Point (subsection 3) and an area located adjacent to the HPSMR (subsection 11b). Effort in subsections 3 and 14b was the greatest during the first survey near the season opening while subsection 11b surrounding the HPSMR

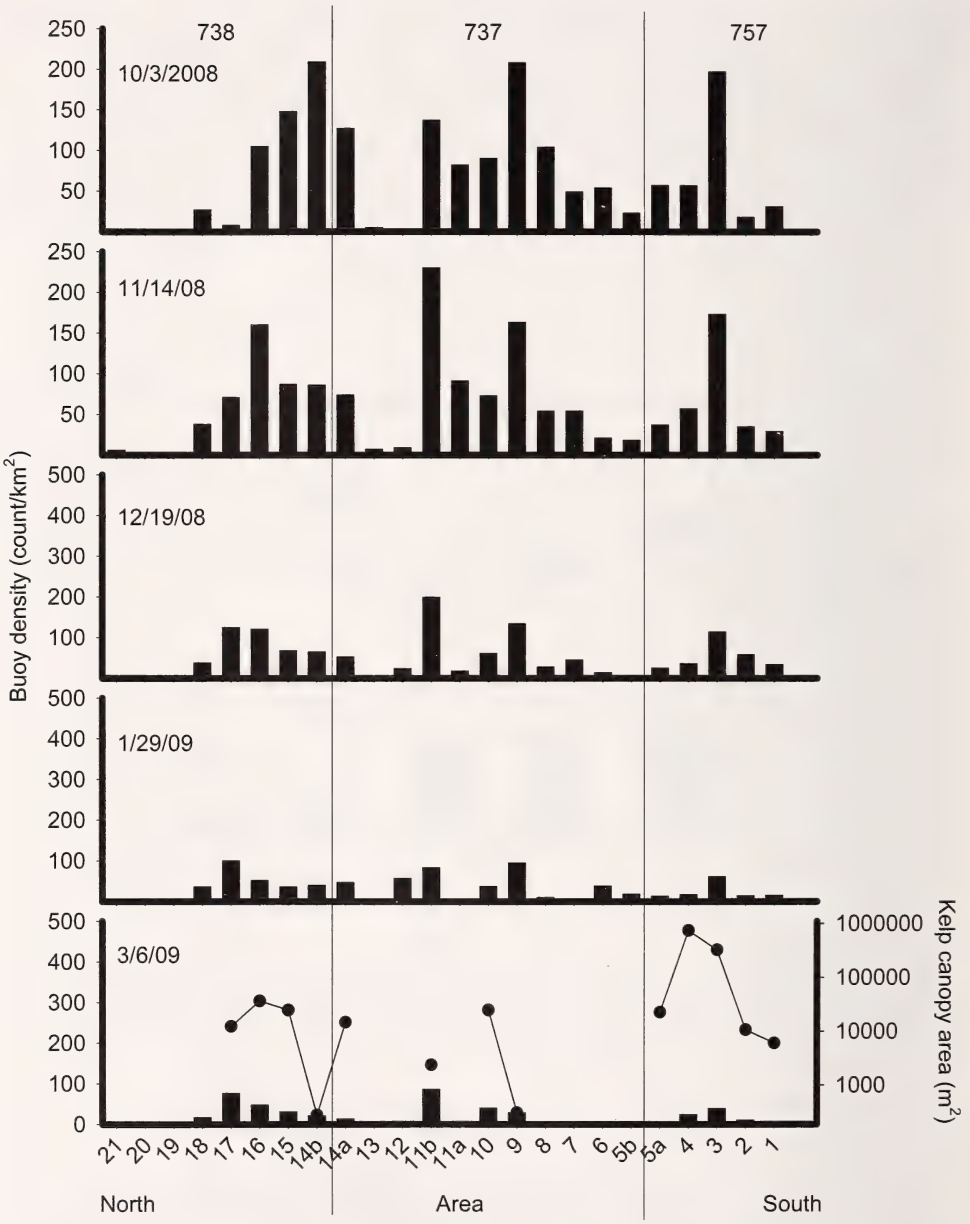

Fig. 3. California spiny lobster trap marker buoy density in each subsection of the three fishing blocks depicted in Figure 1 by survey date during the 2008–2009 commercial fishing season. The Heisler Park no-take marine reserve is subsection 11a. Maximum annual giant kelp canopy (m^2) observed during 2008 in each subsection is represented. Note the log scale for kelp canopy.

received the greatest effort during the next two surveys. Subsections 3, 9, and 11b remained the most productive throughout the season but each declined as the season progressed. Some buoys were recorded within the no-take reserve. Whether these represented traps set within the boundaries or simply a case of the buoy drifting into the reserve while the trap was set outside of the boundary could not be verified.

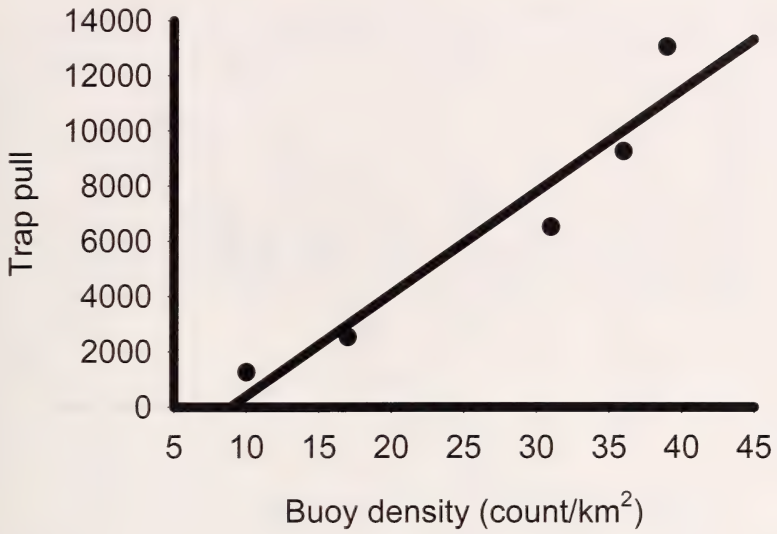

Fig. 4. Scatterplot of the number of commercial California spiny lobster traps pulled, as reported via the California Department of Fish and Game-required commercial fishing logbook, versus the buoy density (count/km^2) summed across the three fishing blocks depicted in Figure 1 and monitored during the 2008–2009 commercial fishing season. The best-fit regression is drawn ($R^2 = 0.93$).

Thirteen of the 24 subsections contained reef habitat as suggested by the presence of a giant kelp canopy (Figure 1). All five subsections in block 757 were within the boundary of the Dana Point-Salt Creek kelp forest as represented by the presence of a canopy. The overall maximum canopy area was in subsection 4 with 0.743 km^2, although this area lies outside of the soon-to-be implemented MPA complex which will primarily encompass block 737. Subsection 3, however, had the greatest proportion of its area covered by giant kelp canopy (Figure 3). The HPSMR (subsection 11a) had no kelp canopy while the adjacent offshore and southeast area (subsection 11b) had a small area of kelp canopy (Figures 1 and 3). No surface canopy was observed to the northwest of the HPSMR within block 737 until the North Laguna kelp bed which covers subsections 14a (block 737) through subsection 17 in block 738. Spearman rank correlation analysis found a significant correlation ($p < 0.05$, $n = 24$) between each survey-specific buoy density by subsection and the associated kelp canopy. With the exception of the January 2009 survey, correlation coefficients (r) steadily increased from 0.53 for the October 2008 survey through 0.72 for the March 2009 survey.

A significant relationship ($R^2 = 0.92$, $F = 32.349$, df = 1,3, $p = 0.011$) was detected between the number of traps pulled reported by commercial fisherman and the buoy densities in all three surveyed blocks, combined, during the 2008 season (Figure 4). The degree of agreement between the two effort measures ranged from block 737 ($R^2 = 0.97$, $p = 0.002$) to block 738 ($R^2 = 0.86$, $p = 0.025$). Total effort was highest in block 757 in during the 2008 fishing season (Figure 2a), which likely related to the differences in size between the three blocks (Figure 1). Effort significantly responded to the legal-sized CPUE with the greatest effort occurring when legal-sized individuals were commonly taken, but declined linearly when the legal-sized CPUE declined (Figure 5; $R^2 = 0.23$, $F = 9.995$, df = 1,34, $p = 0.003$).

The fishery-dependent data was not standardized to area. Logbook records for the Laguna Beach area indicated CPUE for both legal-sized and sublegal-sized individuals

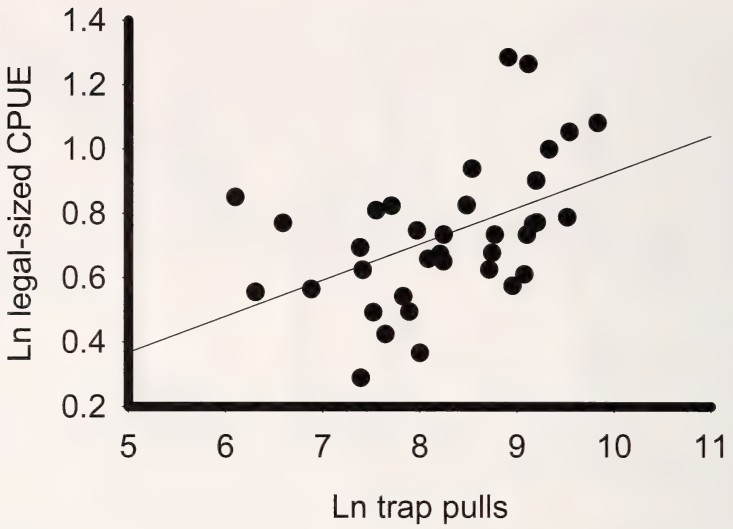

Fig. 5. Scatterplot of the number of commercial California spiny lobster traps pulled, as reported via the California Department of Fish and Game-required commercial fishing logbook, versus the legal-sized catch per unit effort (CPUE; count/trap) for the three fishing blocks depicted in Figure 1 for the 2007–2008 and 2008–2009 commercial fishing seasons, after Ln-transformation. The best-fit regression is drawn ($R^2 = 0.23$).

declined each year as the season progressed (Figure 6); often in similar significantly correlation fashion ($R^2 = 0.65$, $p < 0.001$; Figure 7). The effect of this simultaneous decline on the subsequent season was examined. Each season began with similar CPUEs for legal-sized (~ 0.7 individuals/trap) lobsters, with the exception of 2004. The October 2004 CPUE was significantly higher (ANOVA, $F = 9.731$, $df = 9,20$, $p < 0.001$) than the remaining years, but no differences were detected between any other combination of years.

Discussion

Despite the potential use of pop-up devices to minimize buoy visibility, the significant relationship between buoy densities and the number of traps pulled reported by the commercial fleet (Figure 4) validate the use of buoy counts as a fishery-independent monitoring technique. Using the combination of this and fishery-dependent logbook information, the Orange County lobster fishery was reviewed to determine the spatial distribution of effort. Although catch has been reported and fishing practice is known anecdotally, the density and location of traps set at any time during the season off Orange County, California has not been well documented. Observations of commercial lobster fishing in Orange County suggested that fishing effort was most intense at the beginning of the season, with effort declining as the season progressed. Because of minimum size requirements for the legal take of lobster, harvestable individuals should be most abundant early in the season as a result of growth during the seasonal closure. Observed fishing effort (Figure 2a) and commercial logbook information (Figure 6) concur with this hypothesis. All available measures of effort suggest that as the catch declines, fishing effort correspondingly declines (Figure 5).

More important than the sheer number of traps is their distribution throughout the area. Adult California spiny lobsters prefer high-relief rocky habitat (Barsky 2001). While

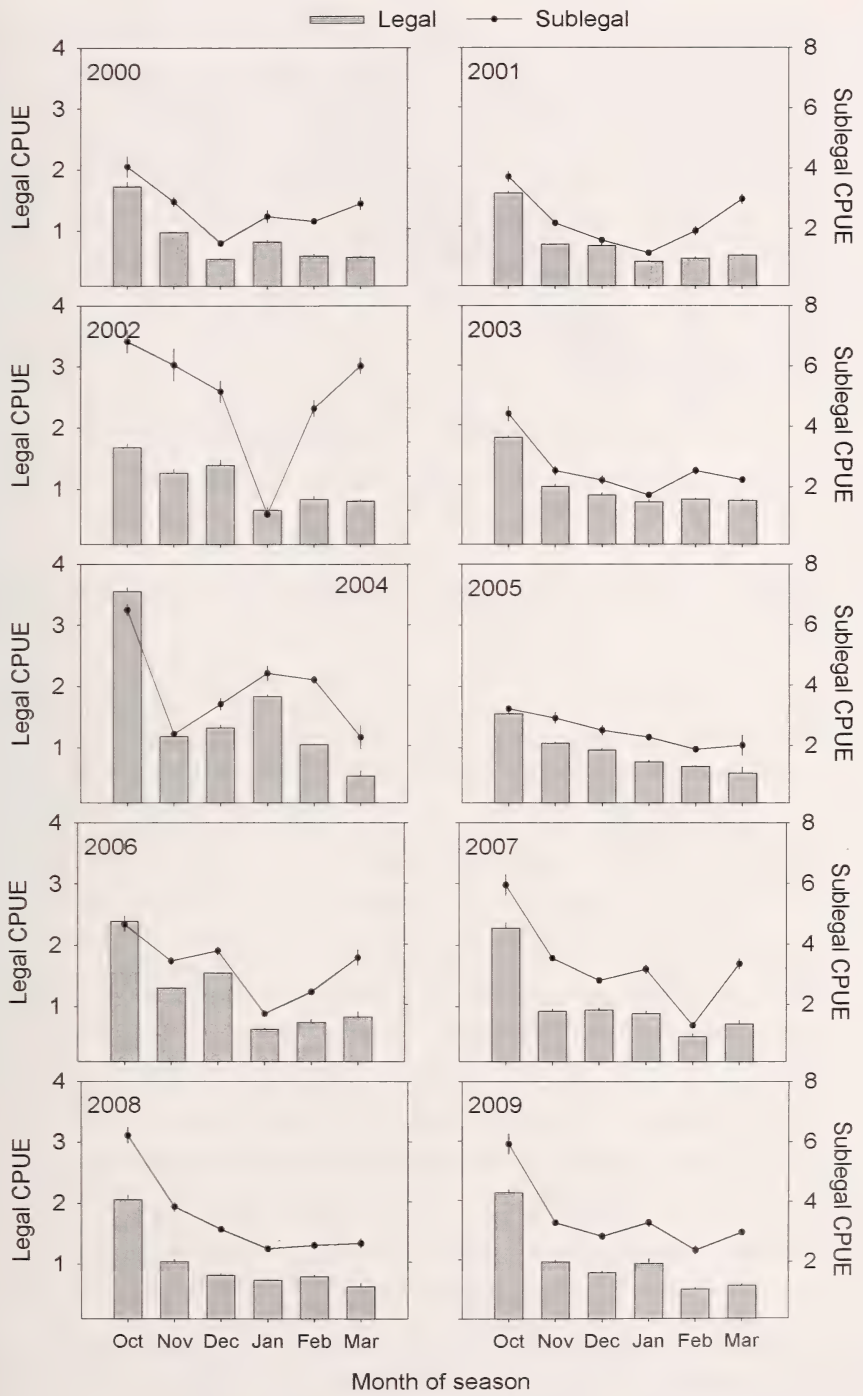

Fig. 6. The legal-sized and sublegal-size California spiny lobster catch per unit effort (CPUE; count/trap) as reported via the California Department of Fish and Game-required commercial fishing logbook during each of the 2000–2009 commercial fishing seasons.

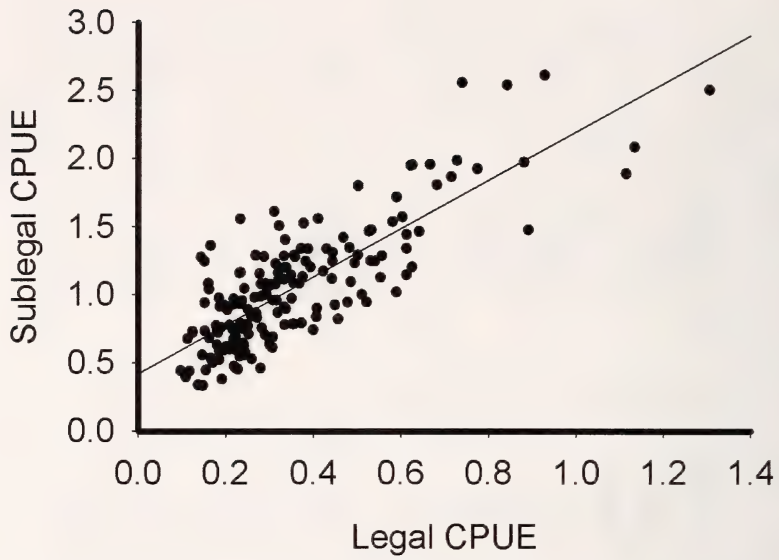

Fig. 7. Scatterplot and linear regression comparing the sublegal and legal lobster CPUEs recorded in fishing blocks 737, 738, and 757 off the Laguna Beach area, 2000–2009. The best-fit regression is drawn ($R^2 = 0.65$).

no subtidal habitat assessments were conducted during this study, the spatial distribution of giant kelp canopy can act as a proxy for hard substrate given giant kelp's general ecological need for hard substrate to anchor its holdfast (Dayton 1985). Furthermore, the significant correlations observed during each survey between the spatial distribution of buoys and kelp canopy in light of the aforementioned substrate preferences of both giant kelp and lobster was consistent with Parnell et al. (2007) who found lobsters, and fishing effort, more commonly on rocky reefs offshore of La Jolla, California.

As noted previously, the commercial fleet in the area reduced effort when the CPUE declined and therefore likely focused remaining effort on the most productive areas which were often associated with above average kelp canopies. These patterns were evident in the subsection buoy densities (Figure 2) and the significant correlations between these densities and kelp canopy area. This is consistent with Parnell et al. (2007) and Parnell et al. (2010) who found the most heavily fished areas were likely highly productive and areas of preferred habitat. As the season progressed, with the exception of January 2009, fishermen progressively abandoned the areas devoid of kelp canopy and increasingly focused their efforts to areas covered to a varying extent by kelp canopy likely due to the presence of submerged hard habitat. The comparatively elevated effort recorded near the southeastern edge of the HPSMR, especially after the first month, suggests that once the abundance of legal-sized individuals was greatly diminished in the areas available to harvest effort, fishermen targeted the edge of the HPSMR where suitable habitat was present as effort in subsection 11b consistently exceeded that in subsection 12 which adjoins the northwest border of the HPSMR. Given lobsters execute nocturnal migrations of up to 1500 m (Hovel and Lowe 2007), it is likely that these migrations potentially exposed them to fishery resources deployed near the reserve boundary similar to that reported by Goñi et al. (2006). This is consistent with fishing effort patterns in similar studies of lobster commercial effort near no-take reserves in southern California, specifically focused effort at reserve boundaries (Parnell et al. 2007; Parnell et al. 2010).

This documented commercial effort in relation to existing no-take marine reserves will likely become more relevant as new MPAs, some of which are no-take reserves, are implemented in southern California[3]. The pending MPA complex in our study area will encompass two of the three most productive sites currently exploited by the commercial fishery, specifically subsections 9 and 11b. This new MPA complex will likely be of sufficient size to allow some individual lobster movement within its borders without being exposed to fishing at the boundary. It will not, however, include the areas of greatest kelp canopy coverage, which will remain open to fishing. Based on the observations near the HPSMR and near the La Jolla Ecological Reserve (Parnell et al. 2007), we anticipate a significant effort along the MPA complex edge. If legal-sized lobster from within the MPA complex are exported out of the no-take area (via migration, density-dependent factors, etc.) as has been described for other spiny lobster species receiving MPA protection (Goñi et al. 2006), then these adjacent areas may become the most productive assuming suitable habitat is present.

Over the 10 commercial seasons studied, the lobster fishery along the southern Orange County coastline began with generally steady catches, excluding 2004, but quickly declined with time likely due to a lack of harvestable individuals as time passed. Surprisingly, sublegal-sized individuals declined at a rate similar to that of the harvestable stock in the Laguna area (Figures 6 and 7). Reasons for this decline are outside the scope of this study, and warrant further examination, but did not appreciably impact the next season's fishery as no significant differences were detected between the October CPUEs in 9 out of 10 seasons. These simultaneous declines and apparent non-impact on the following season superficially resembles what would be expected given the documented behavior of other spiny lobster species (*Panulirus*, *Jasus*). Specifically, a potential explanation includes a mass migration wherein all lobster size classes were observed to move from shallow spawning habitat into deeper waters (Kanciruk and Herrnkind 1978 and references therein; MacDiarmid 1991). Data reported by Parnell et al. (2007) was consistent with this as they documented a shift in effort to deeper waters during the middle of the season off La Jolla, although the total number of traps set was greatly reduced. This spatial shift in effort, small as it was, may be a fishermen adaptation to the offshore migration and consistent with that described by Kanciruk and Herrnkind (1978). Work by Hovel and Lowe (2007) confirmed movement by individual animals, but further research on the seasonal movements is needed to verify the potential similarities between the California spiny lobster and those from the Atlantic and Southern Pacific. Interestingly, Kanciruk and Herrnkind (1978) also reported that the migrating lobsters were typically smaller in size and more frequently sexually-inactive in comparison to those found at shallower depths prior to the migration beginning. Overall, these data suggest that the commercial California spiny lobster fishery in the vicinity of Laguna Beach, California is likely sustainable at this time under the present level of effort.

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A New Species Of Late Cretaceous (Campanian) Cypraeid Gastropod, Santa Ana Mountains, Southern California and New Records of California Cretaceous Cypraeids

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Abstract.—A new species of Cypraeidae is described from the middle Campanian (Late Cretaceous) portion of the Schulz Ranch Member of the Williams Formation, Santa Ana Mountains, Orange County, southern California. This is the first cypraeid described from the Williams Formation and only the second cypraeid species described from the Santa Ana Mountains. New paleogeographic and chronologic records of previously described and indeterminate Cretaceous cypraeid species are also listed.

Introduction

Cretaceous cypraeids are uncommon in North American strata and comprise 17 previously described species (Groves, 1990; 1994; 2004). Of these 17 species, seven are in the genus *Palaeocypraea*, four are in the genus *Bernaya s.s.*, and six are in the genus/subgenus *Bernaya (Protocypraea)*. A new species of *Bernaya (Protocypraea)* is described from the Upper Cretaceous (middle Campanian) Schulz Ranch Member of the Williams Formation, Santa Ana Mountains, Orange County, southern California. This is the first cypraeid species described from the Williams Formation, which brings the North American total to 18. Of these 18 species 12 are from western North America (Table 1).

Stratigraphy and Geologic Age

Popenoe (1937) informally introduced the Schulz member of the Williams Formation as part of a "generalized section of formations in the Santa Ana Mountains, California." The Schulz Member of the Williams Formation of Popenoe (1942) was formally described for outcrops of Late Cretaceous age approximately 0.402 km (0.25 mile) upstream from the mouth of Williams Canyon, near the western boundary of the Schulz Ranch, Santa Ana Mountains, Orange County, California. The member was composed predominantly of coarse-grained, light-colored, cross-bedded arkosic sandstone and minor boulder beds. To eliminate confusion with the Schulz Member of the Talpa Formation of Permian age in Coleman County, Texas, Woodring and Popenoe (1945) revised the name to the Schulz Ranch Member of the Williams Formation.

The new species was collected from a conglomeratic sandstone bed from the basal 4.5–6.0 m (15–20 ft.) of the Schulz Ranch Member above a disconformable contact with the

Table 1. Updated list of Cretaceous cypraeid species from North America and their generalized localities (formation is included for the new species).

PALAEOCYPRAEA
Early Cretaceous
Palaeocypraea fontana (Anderson, 1958) [Shasta Co. California]
Late Cretaceous
Palaeocypraea corsicana (Stephenson, 1948) [Navarro Co., Texas]
P. grooti (Richards and Shapiro, 1963) [New Castle Co., Delaware]
P. nuciformis (Stephenson, 1941) [Navarro Co., Texas]
P. squyeri (Campbell, 1893) [Dawson Co., Montana]
P. suciensis (Whiteaves, 1895) [San Juan Co., Washington]
P. wilfredi Groves, 2004 [Butte Co., California]
BERNAYA s.s* and *BERNAYA (PROTOCYPRAEA)
Late Cretaceous
Bernaya (Bernaya) beardi Groves, 2004 [Vancouver Id., British Columbia]
B. (B.) burlingtonensis (Schilder, 1932) [Burlington Co., New Jersey]
B. (B.) crawfordcatei Groves, 1990 [San Diego Co., California]
B. (B.) jeanae Groves, 2004 [Butte Co., California]
B. (Protocypraea) argonautica (Anderson, 1958) [Jackson Co., Oregon]
B. (P.) berryessae (Anderson, 1958) [Yolo Co., California]
B. (P.) gualalaensis (Anderson, 1958) [Mendocino Co, California]
B. (P.) louellasaulae new species [Williams Fm., Orange Co., California]
B. (P.) mississippiensis Groves, 1990 [Lee Co., Mississippi]
B. (P.) popenoei Groves, 2004 [Orange Co., California]
B. (P.) rineyi Groves, 1990 [San Diego Co., California]

underlying Holz Shale Member of the Ladd Formation. Filkorn (2005) reported the first occurrence of the hippuritid rudist bivalve *Barrettia sparcilirata* Whitfield, 1897 from the Upper Cretaceous of the North American west coast along with the more widely distributed caprinid rudist *Coralliochama orcutti* White, 1885, from the locality. He further reported in 2007 that the fauna also included fragments of an undetermined species of radiolitid rudist. Additional bivalve genera and species at the locality include *Calva*, *Crassatella*, *Cucullaea*, *Glycymerita veatchii* (Gabb, 1864), *Indogrammatodon*, *Opis rosarioensis* Anderson and Hanna, 1935, *Pterotrigonia*, and *Spondylus*. Gastropod genera and species include *Ampullina?, Bernaya* (*Protocypraea*) sp., cf. *B.* (*P.*) *popenoei* Groves, 2004, *Biplica*, *Pentzia*, *Volutoderma santana* Packard, 1922, and an undetermined cerithiid. One paratype of *Prisconatica hesperia* Squires and Saul, 2004, LACMIP 8128, is from LACMIP locality 27199, which is equivalent to the new cypraeid locality LACMIP 17761. It was thought that the specimen represents reworked material from the underlying upper part of the lower Campanian Holz Shale Member of the Ladd Formation (Squires and Saul, 2004). Non-molluscan biota includes several species of colonial scleractinian corals and the calcareous alga *Archaeolithothamnium* sp. Despite containing rip-up clasts from the underlying Holz Shale Member of the Ladd Formation, fossils in the conglomeratic sandstone were mostly unabraded and well-preserved with original shell material. This unabraded condition indicated that they were not reworked and likely only transported a short distance, possibly by a storm surge. Squires and Saul (2009) indicated the stratigraphical range of the bivalve *Opis rosarioensis* Anderson and Hanna, 1935, found here and elsewhere in the Schulz Ranch Member of the Williams Formation, to be lower middle Campanian.

Abbreviations

Abbreviations used for institutional specimen and locality numbers are: CAS, California Academy of Sciences, San Francisco; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; SC, Sierra College, Rocklin, California; SU, Stanford University, Palo Alto, California [collections now housed at CAS]; UCLA, University of California, Los Angeles [collections now housed at LACMIP].

Measurement parameters were defined as: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum.

Systematic Paleontology

The classification used here follows that of Schilder and Schilder (1971).

Superfamily Cypraeoidea Rafinesque, 1815

Family Cypraeidae Rafinesque, 1815

Subfamily Bernayinae Schilder, 1927

Tribe Bernayini Schilder, 1927

Genus *Bernaya* Jousseaume, 1884

Type Species: *Cypraea media* Deshayes, 1835, by original designation. Upper middle Eocene (Bartonian Stage), Auvers-sur-Oise, Val-d'Oise (northwest of Paris), France.

Diagnosis: Shell small to large size; anterior end weakly carinate; dorsum smooth; spire of medium height and partially exposed; aperture wide, sides rounded; anterior and posterior canals deep; fossula smooth, concave, wide.

Remarks: Schilder and Schilder (1971) recognized five species and two subspecies of worldwide Cretaceous *Bernaya s. s.*, and all seven were recognized as full species by Groves (1994). Subsequent to Schilder and Schilder (1971), Yü and Zhu (1983) described a single new species, and Groves (1990, 2004) described three additional species. Although these studies raised the present total to 11 species, only three of the species are from western North America. Groves (2004) documented a poorly preserved specimen of *B. (B.) crawfordcatei* Groves, 1990, from the Campanian Pleasants Sandstone Member of the Williams Formation, the only known *Bernaya s. s.* from the Santa Ana Mountains.

Subgenus *Protocypraea* Schilder, 1927

Type Species: *Eocypraea orbignyana* Vredenburg, 1920, by original designation. Upper Cretaceous (Turonian through Santonian), Trichinopoly Group, Kullygoody, southern India.

Diagnosis: Shell small to large size; moderately pyriform shape, constricted anteriorly; fossula smooth, concave, wide.

Remarks: Schilder and Schilder (1971) recognized eight species and seven subspecies of Cretaceous *Bernaya (Protocypraea)* and all of their subspecies were elevated to specific level by Groves (1994). Subsequent to Schilder and Schilder (1971), three species were described by Groves (1990 and 2004), and another new species is described here. This raises the present total to 19 species, five of which are from western North America. Groves (2004) described *Bernaya (Protocypraea) popenoei* from the lower Campanian Holz Shale Member of the Ladd Formation, the only species of *Bernaya (Protocypraea)* previously known from the Santa Ana Mountains.

Explanation of Figures 1–4. Cretaceous cypraeids from the Santa Ana Mountains: Fig. 1 - *Bernaya (Protocypraea) louellasaulae* new species, holotype LACMIP 13720, from LACMIP loc. 17761, dorsal view (× 3.7). Fig. 2 – ventral view of same specimen. Fig. 3 - *Bernaya (Protocypraea)* sp., cf. *B. (P.) popenoei* Groves, 2004, hypotype LACMIP 13893, from LACMIP loc. 17761, dorsal view (× 3.6). Fig. 4 – ventral view of same specimen.

Bernaya (Protocypraea) louellasaulae new species

(Figs. 1–2)

Diagnosis: *Bernaya* of medium size, anterior and posterior canals deep, spire of medium height, fossula concave, and smooth posterior terminal ridges extend to margins.

Description: Shell of small to medium size, constricted anteriorly; maximum height of shell nearly centered; maximum width of shell slightly posterior of center; dentition coarse to medium with smooth interstices; columellar lip with 11 teeth, labral lip with 15 teeth; aperture fairly wide and straight, curved posteriorly toward columella, widens anteriorly; terminal canals deep; columella slightly inflated; prominent anterior terminal ridges form a slight marginal callus; posterior terminal ridge extended from base of spire to form a slight marginal callus; spire of medium height and partially exposed due to shell loss.

Comparison: The new species resembles *Bernaya (Protocypraea) veraghoorensis* (Stoliczka, 1867) from the Upper Cretaceous (Campanian) Arrialoor Group, near Veraghoor, Tamilnadu District, India, particularly the specimen figured by Stoliczka (1868: pl. 4, fig. 4) [as *Cypraea (Luponia) carnatica*]. In contrast, the new species is less inflated, more constricted anteriorly, and has a narrower and less sinuous aperture than *B.* (*P.*) *veraghoorensis*.

Discussion: Generic and subgeneric assignment are based on the wide aperture, deep anterior and posterior canals, and medium-height spire. *Bernaya (Protocypraea) louellasaulae* represents the first cypraeid described from the Williams Formation.

Type Material: Holotype, LACMIP 13720. A single fairly well-preserved specimen with minor amounts of apparent original shell material on the base and lateral margins. The specimen measures 17.2 mm in length, 10.8 mm in width, and 9.3 mm in height.

Type Locality: LACMIP loc. 17761, Schulz Ranch Member of Williams Formation, near 533 m (1750 ft.) elevation at bottom of eastern tributary to Fremont Canyon, Santa Ana Mountains, Orange County, California. Collectors: John M. Alderson and Harry F. Filkorn, 4 April, 2004.

Etymology: This species is named for LouElla R. Saul (LACMIP, Research Associate) for her numerous important contributions to the paleontology of the western United States.

Additional Records of California Cretaceous Cypraeids

Bernaya (Protocypraea) sp., cf. *B.* (*P.*) *popenoei* Groves, 2004

(Figs. 3–4)

New Record: Hypotype, LACMIP 13893, LACMIP loc. 17761 (see locality description above), Upper Cretaceous Schulz Ranch Member, Williams Formation, collected by John M. Alderson and Harry F. Filkorn, 4 April, 2004. This record is based on a single fairly well-preserved internal mold, that is 25.5 mm in length, 17.7 mm in width, and 13.2 mm in height.

Distribution: This species was formerly restricted to the lower Campanian part of the Holz Shale Member of the Ladd Formation and is here extended upward to the lower middle Campanian part of the Schulz Ranch Member of the Williams Formation.

Bernaya? sp.

New Record: SC MG153, Granite Bay, Treelake Village Estate, northeast of Sacramento, Placer County, California. Upper Cretaceous (Campanian), Chico Formation. Poorly preserved internal mold. Collected by Richard P. Hilton (SC) during paleontological monitoring for land development in 1999.

Cypraeidae, undetermined genus and species

New Record: CAS 69097.03 (*ex* SU 30286), Dip Creek, San Luis Obispo County, California. Uppermost Cretaceous/lowermost Paleocene Dip Creek Formation. A single poorly preserved internal mold. Collected by Nicolas L. Taliaferro, date unknown.

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Appendix 1.

Localities Cited

CAS 69097. Dip Creek, NE ¼ sec. 30, T25N, R10E, U.S. Geological Survey Adelaida 7.5′quadrangle, San Luis Obispo Co., California. Uppermost Cretaceous/lowermost Paleocene, Dip Creek Formation (?). Collector: Nicolas L. Taliaferro, date unknown.

LACMIP loc. 17761. Float blocks of conglomeratic sandstone from basal 4.5–6.0 m (15–20 ft) of member, near 533 m (1750 ft.) elevation at bottom of eastern tributary to Fremont Canyon, center of SW ¼ SW¼ sec. 7, T4S, R7W, U.S. Geological Survey Black Star Canyon 7.5′quadrangle (1967 [PR 1973]), eastern Santa Ana Mountains, Orange County, California. Upper Cretaceous (lower middle Campanian), Schulz Ranch Member, Williams Formation. Collectors: John M. Alderson and Harry F. Filkorn, 4 April, 2004 and 4 April, 2005. This locality is equivalent to LACMIP loc. 27199 (= UCLA 7199) collected by Willis P. Popenoe and J.E. Schoellhammer in 1951.

SC MG153. Granite Bay, Treelake Village Estate, NE ¼ sec. 16, T10N, R7E, U.S. Geological Survey 7.5′ Folsom quadrangle (1967 [PR1975]), northeast of Sacramento, Placer Co., California. Upper Cretaceous (Campanian), Chico Formation. Collector: Richard P. Hilton, 1999.

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Southern occurrence of the sand sole (*Psettichthys melanostictus*).

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The geographic and depth ranges of marine fishes commonly reflect their physiological preferences (Pörtner et al., 2010). Given the wide availability of habitats along the California coastline, biogeographic range extensions of many species have been observed to occur periodically, most frequently during periods of short-term oceanographic temperature fluctuation. Over the last 30 years, these range extensions in California have mostly been poleward expansions as ocean temperatures have warmed or through large-scale oceanographic anomalies such as Californian-El Niño conditions (Lea and Rosenblatt, 2000). Many of the recently documented range extensions in southern California have been associated with thermal power plant cooling water intakes or discharges, often due to the increased sampling and/or the presence of greater-than-ambient water temperatures near the discharges (Pondella, 1997; Lea and Rosenblatt, 2000; Miller and Curtis, 2008). In addition to the thermal discharge, the cooling water system entrains material, including fishes, with the cooling water drawn into the system. The cooling water is filtered through traveling screens with a nominal square mesh of 10-mm to prevent debris from passing farther into the system and potentially clogging downstream condensers. Fish impingement upon these traveling screens is routinely monitored to provide a representative accounting of the fishes taken in by the cooling water system, and an opportunity to collect random tourist species.

Sand sole (*Psettichthys melanostictus*) reportedly ranges from the Southeastern Bering Sea, Alaska to Newport Beach, California in depths ranging from the intertidal zone out to 325 m (Love et al., 2005). Museum records contain numerous specimens taken in northern California with only three lots collected offshore of Ventura County, California at the southernmost extent (Fishnet2 2011). Surprisingly, no records were found for collections in the Santa Barbara, California area despite substantial areas of suitable habitat. Reviews of the Santa Barbara Natural History Museum (SBNHM 2011) ichthyology records found no sand soles in the collection. Fitch and Schultz (1978) detailed two fish taken in the southern Santa Monica Bay in the mid-1970s during impingement sampling at Scattergood Generating Station in El Segundo, California and the Redondo Beach Generating Station in Redondo Beach, California. The Redondo Beach sample had set the southern range limit for this species at the time. Slightly farther southwards, several sand sole were caught by recreational anglers fishing off the Balboa Pier during the 1980s (M. Love, unpubl. data), which had served as the impetus for the current southern range endpoint. One collection that has gone largely unreported is recorded in the Museum of Comparative Zoology (MCZ 2011) as collected in San Diego County, California during the mid-1800s (Lot 25988) and has not been previously included in the biogeographic distribution of the sand sole (Love et al., 2005; Horn et al., 2006). This sample, however, has limited information regarding its collection. Careful

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Fig. 1. Photo of a sand sole collected at the San Onofre Nuclear Generating Station near San Clemente, California on March 22, 2011. The specimen measured 235 mm SL and weighed 212 g.

review of the available record indicates the sample is now missing and was originally held in a jar with other lots collected near San Francisco, California (Lots 11197 and 11559) that each contain extensive collection information. The status of this San Diego record raises concerns as to its validity given the lack of collection information, unknown present status of the specimen, and its historic storage with San Francisco collections.

While these records hardly represent its population size in the area, it does signify the rarity of its occurrence in the Southern California Bight. A demersal species, it has yet to be taken in either of the four completed summer regional otter trawl surveys conducted by the Southern California Coastal Water Research Project (E. F. Miller, pers. obs.) or in various otter trawl monitoring surveys conducted on a near annual basis since 1972 throughout portions of the Southern California Bight in support of regulated discharge monitoring (Stull and Tang, 1996).

The San Onofre Nuclear Generating Station Unit 2 withdraws seawater through an open-water intake located 950 m offshore along the 10-m isobath at 33° 21.633′N, 117° 33.743′W. On March 22, 2011, R.H. Moore collected a 235-mm SL sand sole that weighed 212 g (Figure 1) during an impingement survey. The identification was made based on the occurrence of five free dorsal rays, consistent with the diagnostic features described by Miller and Lea (1976) and confirmed with local taxonomic experts (H.J. Walker, pers. comm.[2]; R.N. Lea, pers. comm.[3]; M.L. Love). This specimen has been deposited with the Scripps Institution of Oceanography Marine Vertebrate Collection with catalog number SIO 11–74.

We note that the San Onofre fish represents the most southerly physical collection of this species. However, on 3 September 2009, a specimen was photographed *in situ* in the La Jolla Shores area (at about 32° 51.3′N, 117° 15.2′W) at a depth of about 20 m by David Andrews (Figure 2). The identity of this specimen was confirmed by M.L. Love based on the dorsal fin ray separation. Thus the documented range of the sand

[2] H.J. Walker, Jr. Collection Manager, Scripps Institution of Oceanography Marine Vertebrates Collection

[3] R.N. Lea, California Department of Fish and Game, Retired.

Fig. 2. Image of sand sole observed in the La Jolla Shores, California area at a depth of ~ 20 m taken on September 3, 2009 by D. Andrews with the identity confirmed by M. L. Love.

sole has been extended/reconfirmed southwards approximately 105 km from Newport Beach to La Jolla Shores, California. This may represent the second record from the San Diego County, California area separated by over 100 years if the aforementioned mid-1800s specimen catalogued in the Museum of Comparative Zoology is considered, but, again, the earlier sample is unconfirmed and questionable given the caveats detailed above.

Recent southern extensions or occurrences have been noted less frequently given the recent poleward trend in biogeographic shifts (Lea and Rosenblatt, 2000; Perry et al., 2005; Harley et al., 2006), but the recent decline in seawater temperatures (Figure 3) may have made southern extensions, such as this, physiologically possible. Mean annual sea surface temperatures (SST) recorded at the San Clemente Pier in San Clemente, California, approximately 8 km northwest of the San Onofre Nuclear Generating Station, through September 30, 2010 were the third coolest since 1990 and the 16th coolest since 1966 (UCSD 2011). With the exception of 2004 and 2009, the mean annual SST since 2000 at San Clemente has remained below 17.5°C after generally exceeding this for the prior 17 years. If oceanographic conditions continue as they have persisted for the recent five years, it is expected that additional southern range extensions will be recorded.

Acknowledgements

We would like to thank Southern California Edison and the San Onofre Nuclear Generating Station for their support of the impingement monitoring program.

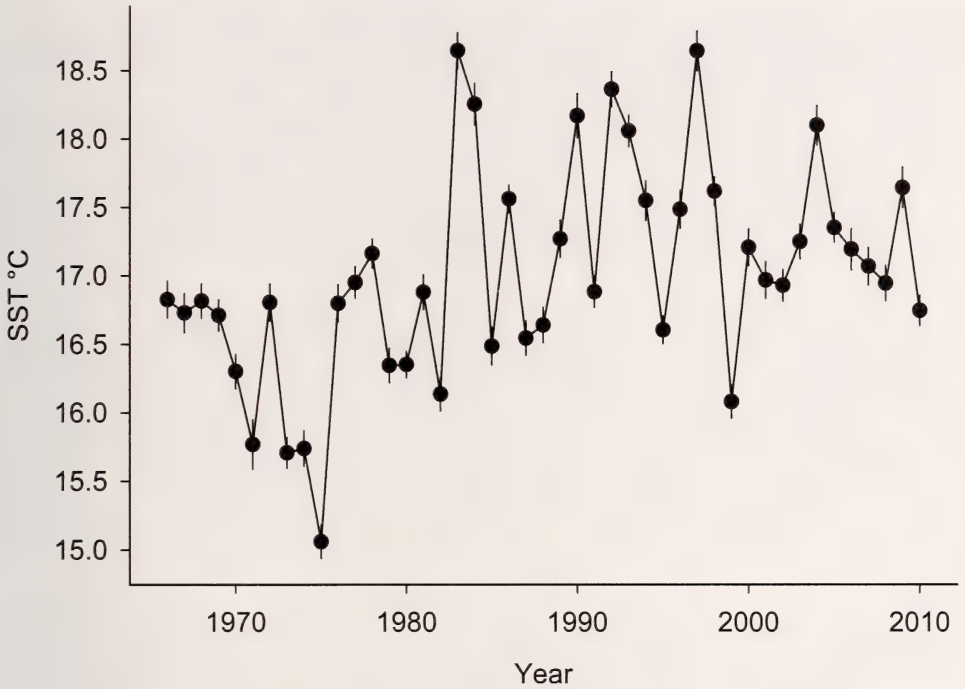

Fig. 3. Mean daily sea surface temperature (°C) recorded at the San Clemente Pier, San Clemente, California, approximately 8 km northwest of the San Onofre Nuclear Generating Station, January 1, 1966 – September 30, 2010.

Additional gratitude is extended to H.J. Walker, Jr. and R.N. Lea for their assistance with confirming the identification. R. Feeney provided invaluable assistance in our search for museum collections. The comments of two anonymous reviewers and extensive discussion with R.N. Lea substantially improved this manuscript.

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Reproduction in the Great Basin Collared Lizard, *Crotaphytus bicinctores* (Squamata: Crotaphytidae)

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Abstract.—The reproductive cycle of the Great Basin Collared lizard, *Crotaphytus bicinctores* was studied by a histological examination of museum specimens. Mean clutch size (n = 13) was 3.46 ± 1.1 SD, range: 2–6. Histological evidence indicates that two clutches may be produced in the same year. The reproductive season includes spring and early summer. There was a significant positive correlation between female body size (SVL) and clutch size (P = 0.03). The smallest reproductively active male and female C. bicinctores measured 81 mm and 78 mm SVL, respectively.

Crotaphytus bicinctores frequents xeric rocky habitat in southeastern and extreme northeastern California, much of Nevada, western and northern Arizona, western and central Utah, southeastern Oregon and western Idaho (McGuire 1996). Information on its reproduction is limited and consists of reports of juveniles, gravid females and adult males from southeastern California on 2 May (McGuire 1996); neonates observed in eastern Oregon in August (Brooking 1934); mean clutch size of 5.38, (range: 3–7), egg deposition in June in Millard County, Utah (Andre and MacMahon 1980). Ryan (2009) reported clutch sizes of 3–7, the possibility of 2 clutches and hatchlings appearing in August (Ryan 2009). The purpose of this paper is to examine the reproductive cycle of *C. bicinctores* in the southern portion of this species range. Information on the reproductive life history including period of sperm production, timing of yolk deposition and number and sizes of clutches produced, provides critical information for formulating conservation policies of lizard species populations. Due to the difficulty in justifying collections of monthly lizard samples, utilization of museum collections for obtaining reproductive data has become increasingly important.

A sample of 135 *C. bicinctores* consisting of 57 adult males (mean snout-vent length [SVL] = 94.5 mm ± 7.7 SD, range: 81–117 mm; 47 adult females (mean SVL = 88.5 mm ± 5.9 SD, range: 78–98 mm); 31 subadults consisting of 15 males (mean SVL = 67.8 mm ± 6.5 SD, range: 58–78 mm SVL) and16 females (mean SVL = 67.1 mm ± 6.5 SD, range: 56–75 mm SVL) from Arizona (n = 5), California (n = 114), Nevada (n = 14) and Utah (n = 2) was examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM: Appendix 1). Lizards were collected from 1929–1980.

The left testis was removed from males and the left ovary was removed from females for histological examination (Presnell and Schreibman 1997). Enlarged ovarian follicles (> 5 mm) and/or oviductal eggs were counted. Tissues were embedded in paraffin, sectioned at 5 μm and stained with hematoxylin followed by eosin counterstain. Slides of testes were examined to ascertain the stage of the testicular cycle. Slides of ovaries were

Cover Page Footnote: We thank Christine Thacker (LACM) for permission to examine specimens.

Table 1. Monthly stages in the testicular cycle of 57 *Crotaphytus bicinctores*.

Month	*n*	Regression	Recrudescence	Spermiogenesis
March	5	1	2	2
April	18	1	5	12
May	17	1	4	12
June	9	1	0	8
July	4	1	1	2
August	4	4	0	0

examined to ascertain the stage of the ovarian cycle. Histology slides were deposited in the herpetology collection of LACM. Mean SVL of male and female *C. bicinctores* were compared using an unpaired *t*-test and the relationship between female SVL and clutch size was examined using linear regression analysis (Instat vers. 3.0b, Graphpad Software, San Diego, CA).

The mean SVL of males of *C. bicinctores* significantly exceeded that of females (unpaired *t* test, $t = 4.4$, $df = 102$, $P < 0.0001$). Monthly changes in the testicular cycle of *C. bicinctores* are shown in Table 1. Three stages were present: (1) Regression, the germinal epithelium is reduced to 1–3 cell layers in thickness and consists of spermatogonia and Sertoli cells; (2) Recrudescence, a proliferation of germ cells for the next period of sperm formation is underway. In early recrudescence, primary spermatocytes predominate, whereas in late recrudescence, secondary spermatocytes and spermatids are most abundant; (3) Spermiogenesis, lumina of the seminiferous tubules are lined by clusters of sperm or metamorphosing spermatids. The period of sperm production encompassed March to July. The smallest reproductively active (spermiogenic) male of *C. bicinctores* (LACM 16870) measured 81 mm SVL, and was collected May 1954 from Los Angeles County. Males < 81 mm SVL had not attained reproductive maturity.

Monthly changes in the ovarian cycle of *C. bicinctores* are presented in Table 2. Four stages were present in the ovarian cycle of *C. bicinctores*: (1) No yolk deposition (quiescent); (2) Early yolk deposition with basophilic granules present in the ooplasm; (3) Enlarged preovulatory follicles (> 4 mm); (4) Oviductal eggs. Gravid females were noted April to June. Mean clutch size ($n = 13$) was 3.46 ± 1.1 SD, range: 2–6. Linear regression analysis revealed a significant positive correlation between female SVL (n = 13) and clutch size ($Y = -4.95 + 0.095X$, $r = 0.57$, $P = 0.04$). A significant positive correlation between female SVL and clutch size was also reported for *C. bicinctores* from Millard

Table 2. Monthly stages in the ovarian cycle of 47 *Crotaphytus bicinctores*, * = one female with oviductal eggs and concurrent early yolk deposition for a second egg clutch; ** = some enlarged follicles in one female were crushed not allowing clutch determination.

	n	Quiescent	Early yolk deposition	Enlarged follicles > 5 mm	Oviductal eggs
April	8	6	1	0	1
May	23	9	8	4	2
June	6	0	0	5**	1*
July	3	3	0	0	0
August	6	5	1	0	0
October	1	1	0	0	0

County, Utah (Andre and MacMahon 1980). The smallest reproductively active female (LACM 26840) measured 78 mm SVL, contained three oviductal eggs and was collected June 1958 in Churchill County, Nevada. Females < 78 mm SVL had not attained reproductive maturity. One female (LACM 16865) from Los Angeles County collected 14 June (SVL 93 mm) contained three oviductal eggs and concurrent early yolk deposition for a subsequent clutch indicating select females may produce two clutches in the same reproductive season. A single female collected in August exhibited early yolk deposition (Table 2), but it is not known if she would have produced a clutch or if the follicles would have undergone atresia. Follicular atresia is commonly observed near the close of the reproductive season when follicles that did not complete vitellogenesis degenerate (Goldberg 1973).

Andre and MacMahon (1980) reported a mean clutch size of 5.38, (range 3–7) for six females from northern populations from Idaho and Utah. Fitch (1985) reported a mean value of 5.0, range 3–8 for six northern *C. bicinctores* females from southern Idaho and Millard and Tooele counties, Utah. Both values for northern *C. bicinctores* females were greater than those of Fitch (1985) for seven females from southern populations in California, Nevada and Utah (3.9, range 2–5), suggesting larger clutch sizes at higher latitudes. The value provided by Fitch (1985) for southern populations approximates our value (n = 13, 3.46 ± 1.1 SD, range 2–6) reported herein. Whether the larger clutch sizes in *C. bicinctores* from northern populations reflect a shorter activity season with fewer females producing two clutches, warrants further study.

Other species of *Crotaphytus* exhibit similar reproductive life histories. *Crotaphytus vestigium* exhibited a spring to early summer period of sperm production and ovarian activity (Goldberg and Mahrdt 2010) as did *Crotaphytus collaris* (Fitch 1956, Trauth 1978, 1979). Two clutches were produced by *C. collaris* in Arkansas (Trauth 1978). Based on anecdotal information such as time of egg deposition and appearance of hatchlings, other species of *Crotaphytus* also appear to exhibit similar timing of events in their breeding cycle, even though their reproduction has not been studied in detail. The report of a gravid female of *Crotraphytus grismeri* from September (McGuire 1996) merits further investigation. Detailed studies of the breeding cycles of *C. antiquus, C. dickersonae, C. grismeri, C. insularis* and *C. nebrius* (see McGuire 1996, Grismer 2002, Babb 2009) are needed to ascertain similarities in the timing of the reproductive cycles, and also to determine if significant geographic variation in their clutch sizes exists.

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Appendix I

Crotaphytus bicinctores examined from the Natural History Museum of Los Angeles County (LACM) by state and county: **Arizona**: Coconino 134075; Yuma 16892, 16893, 26835, 26836; **California**: Inyo 26824–26832, 36666, 36667, 36670, 52887, 122468, 123321–123325; Kern 63829–63835, 63837, 63838; Los Angeles 3994–3996, 3998, 3999, 16865, 16867, 16870, 16872, 26811, 26812, 26814, 26815, 63188–63190, 94595–94600, 132436, 132437; Riverside 16876, 16885, 16888, 16889, 26820, 26822, 62448, 94601–94624, 94626; San Bernardino 16877, 16882, 16883, 21651, 23245, 26816–26819, 63179, 63180, 63184–63186, 64007, 94633–94638, 94641–94643, 94645–94648, 137887, 137890; **Nevada**: Churchill 26840–26843; Clark 76458, 107189 Lyon 26837, 26838; Mineral 126915; Nye 61454, 94658, 94659, 133205; Pershing 112790; **Utah:** Washington 94678, 147476.

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